SYNTOPIC COEXISTENCE AND HABITAT USAGE IN TWO MORPHOLOGICALLY SIMILAR *PLETHODON* SPECIES

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Abstract

Numerous studies have shown terrestrial salamanders of similar size compete strongly for cover objects on the forest floor. The cover objects provide a refuge that allows the owner more foraging opportunities throughout the year. Usually the competition between species is asymmetric and results in the exclusion of one of the species from large areas. In Hoosier National Forest, *Plethodon cinereus* and *P. dorsalis* coexist broadly and appear to share the same microhabitats. A number of factors might explain this unique case of coexistence. *P. cinereus* is more common in drier habitats and becomes more predominant as spring becomes warmer and drier compared to *P. dorsalis*. *P. dorsalis* is more common in the moister habitats, and predominates early in the spring. *P. cinereus* also looses water more slowly compared to *P. dorsalis*. Although *P. cinereus* is larger and shows higher levels of aggressive behaviors associated with cover object defense, *P. dorsalis* is better able to hold ownership of cover objects in the lab. The coexistence may be the result of the greater physiological tolerance of *P. cinereus* to drier conditions, which allow it to feed in habitats and at times unavailable to *P. dorsalis*. As conditions on the forest floor get warmer and drier as spring progresses, the more sensitive *P. dorsalis* has to retreat underground sooner than *P. cinereus*. *P. cinereus* will then have foraging opportunities under cover objects that are unavailable to *P. doralis* due to its sensitivity.

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Introduction

Community structure and the maintenance of diversity have long been central themes of community ecology (e.g., Gause 1934). Numerous mechanisms have been shown empirically or theoretically to contribute to the maintenance of species diversity. These include Hubbell's (2001, Volkov et al. 2003) "unified neutral theory of biodiversity and biogeography," building on earlier work on island biogeography (Simberloff 1976) and, in contrast, non-equilibrium dynamics generated by species interactions in complex communities (Huisman and Weissing 2000; Lundberg et al. 2000,). A tradeoff between competition and dispersal in a patchy meta-population environment also can allow the coexistence of competitors (Levins 1969). Other approaches focus more on (near) equilibrium local interactions that allow closely related species to coexist. These include resource partitioning (e.g., Inouye 1999, MacArthur 1958), interactions across diverse resource dimensions (Munday 2001), and character displacement (e.g., Dayan and Simberloff 2005, Yom-Tov et al. 1999) and other forms of interspecific disarmament (Kisdi 2001).

Community structure has been widely studied in North American lungless salamanders of the family Plethodontidae. They are easy to sample, are often abundant and are amenable to a variety of experimental field and laboratory studies (for the classic review see Hairston 1987). One common finding has been strong

competition. Consequently, similar-sized congeneric species usually are allopatric, have narrow zones of sympatry or are sympatric but ecologically segregated (Hairston 1987).

In marked contrast to this generalization, the distributions of two similar-sized species of *Plethodon* overlap broadly in Indiana. The range of *Plethodon cinereus,* the northern red-backed salamander, extends throughout Indiana with the exception of the prairie pocket in northwestern Indiana. The Indiana range of *Plethodon dorsalis*, the northern zigzag salamander, is primarily in the unglaciated hills of the southern third of Indiana, although its range extends in a broad band to the northwest, especially along rocky canyons (Minton 2001). The geographic overlap between these two species is broader than that between any other pair of similar-sized congenerics in the family in eastern North America (Conant and Collins 1998).

Thurow (1955) studied *P. cinereus* and *P. dorsalis* in south-central Indiana. He suggested that *P. dorsalis* was physiologically less tolerant to xeric conditions and was restricted to wet seeps and ephemeral stream beds whereas *P. cinereus* was common in the deeper forest soils. He concluded that the two species did not compete since they lived in different habitats. However, our initial field observations in Brown and Monroe Counties suggested broad syntopic (literally together in a place, that is, sharing the same microhabitat) coexistence. This appeared to be contrary to Thurow's conclusion and distinctly in contrast to the patterns typically reported for other pairs of similar-sized North American plethodontids.

This preliminary work raised key questions regarding the occurrence of these two species. First, what is the extent of overlap in habitat use across the range of more mesic and more xeric habitats? Second, if there are broad overlaps in habitat use, are there differences in microhabitat use (such as types of cover objects) that allow coexistence? That is, both species might overlap broadly on a coarse scale, but microhabitat differences could still allow coexistence.

Substantial prior work on *Plethodon* suggested a number of additional factors that might be relevant to the extent of syntopy. One important factor is sensitivity to desiccation. *Plethodon* are small and elongate, with a consequent large surface to volume ratio. They are also lungless, and respire primarily through their skin and, thus, must keep their skin moist. These factors combine to make *Plethodon* especially sensitive to moisture loss and they frequently are restricted in their activity periods and habitats due to their need to stay cool and moist (Feder 1983).

Differences in local distribution of similar sized *Plethodon* sometimes reflect, in part, differences in desiccation tolerance. Jaeger (1971) showed for two small plethodons that one, *P. shenandoah,* was restricted to rocky talus outcrops, while the other, *P. cinereus,* was common in the deeper forest soils. Similarly, when compared with *P. cinereus*, a second species, *P. wehrlei,* was found in drier habitats and laboratory testing revealed a higher tolerance to desiccation and a lower rate of water loss (Pauley 1978).

Two key questions follow for the *P. dorsalis* and *P. cinereus* system in Indiana. How do the species differ in desiccation physiology? And, how are any

such differences reflected in habit use or other aspects of biology in the zone of sympatry?

Differences in local distribution of similar-sized *Plethodon* often reflect, in part, differences in aggressive behavior. Within a species, Mathis (1990) found that better competitors, the bigger individuals in her study, occupied bigger cover objects. She concluded that larger cover objects offered better buffers to desiccation, and were therefore more valuable. This has been supported by work showing larger *P. cinereus* individuals are more aggressive than smaller individuals (Townsend and Jaeger 1998), although smaller individuals may be able to hold territories if they have the advantage of residency (Townsend et al. 1998).

Between *Plethodon* species, aggression can interact with physiological tolerance. The restriction of *P. shenandoah* to rocky talus slopes was the result of its behavioral exclusion by a more aggressive species, *P. cinereus*, from deeper forest soils where both species could live in the absence of interspecific competition (Jaeger 1981, 1984, Jaeger et al. 1982). *P. cinereus* could not persist in the talus areas due to its greater sensitivity to desiccation (Wrobel et al. 1980).

Aggression can also interact with differences in habitus to allow *Plethodon* species to coexist in a patchy environment. In a study of two large *Plethodon* (Marshal et al. 2004), *P. petraeus* was associated with patchily distributed cave openings and rocky outcrops, while *P. glutinosus* was abundant in the deeper forest soils. In this case, *P. glutinosus* was more aggressive and appeared to be a superior competitor, relegating *P. petraeus* primarily to patchy, rocky habitat that *P.*

glutinosus appeared unable to colonize due to relatively poor climbing ability (Marshal et al. 2004).

In a case of fine-scale coexistence, the larger and more aggressive *P. glutinosus* relegated *P. kentucki* to smaller cover objects. In addition, conspecific aggression and hence, conspecific competition was stronger in each species compared to levels of interspecific aggression (Marvin 1998). This pattern of competition was thought to allow coexistence in accord with the classic Lotka-Voltera model.

In laboratory behavioral trials, a comparison of the time spent in aggressive behaviors relative to submissive or neutral behaviors can provide a proxy measurement of how important of a threat the intruder presents to a resident. *P. cinereus* respond significantly more aggressively to other males than to females (Jaeger at al. 1982). *P. cinereus* reacts aggressively to both other *P. cinereus* and other similar sized species as well (Lancaster and Jaeger 1995, Wrobel et al. 1980) but does not respond aggressively to salamanders of markedly different size (Jaeger et al. 1998). In the latter study, *P. cinereus* responded aggressively to *P. glutinosus* juveniles that were of similar size, but not to the much larger adults. These studies suggest comparing the amount of aggressive behavior does provide a relative measure of potential competition.

This prior work on levels of aggressive behavior and on cover object defense leads to several questions pertinent to the *P. dorsalis* and *P. cinereus* system. Do the species differ in levels of conspecific and interspecific aggressive behavior? How are any such differences related to the pattern expected to lead to

coexistence under the classic Lotka-Voltera model (i.e., coexistence is possible only when conspecific competition is stronger than interspecific competition)? Do the species differ in their ability to hold or invade cover objects in the field or laboratory? If so how are these related to any differences in aggressive behavior?

The interspecific dynamics should also demonstrate the relative ability of each species to colonize empty cover objects, successfully defend cover objects, and successfully usurp residents and gain control of cover objects. The more aggressive species should be better able to maintain residency and possibly usurp residents. In a system of broad syntopic coexistence, which is unknown in the *Plethodon* literature, the effects might be small and might be reflected in the size ratios of residents and usurpers. Intruders into occupied cover objects should be larger than residents in order to overcome the advantage of residency. Intruders into newly empty cover objects often should be smaller than the prior resident presumably reflecting the fact that the larger resident had been excluding the smaller intruders.

Summary of questions addressed and studies undertaken

A series of field and laboratory studies were designed to explore sympatry and syntopy in the *P. cinereus* and *P. dorsalis* system in south-central Indiana. Collectively, these studies address the questions raised above. These main questions with the initial hypotheses are as follows.

1. What is the extent of overlap in habitat use across the range of more mesic and more xeric habitats? Given the earlier work with these two species and the

results of studies of several other pairs of *Plethodon* species, the initial hypothesis was that *P. dorsalis* would be largely restricted to more mesic sites and more patchily distributed. A *habitat plot survey* (Heyer et al., 1994) was designed to examine the extent of habitat use overlap across an array of habitats at a landscape level.

2. If there are broad overlaps in habitat use, are there differences in microhabitat use (types of cover objects or moisture levels under them) that allow coexistence? Given prior work, the initial hypothesis was that *P. dorsalis* would be restricted to more mesic microhabitats. Such a difference would be compatible with differences found for other pairs of *Plethodon*. A *cover object survey* (Heyer et al., 1994) was designed to determine if there were differences in microhabitat use that could explain the coexistence.

3. Does the desiccation physiology differ in ways that could explain the coexistence? Given the prior work with these species in southern Indiana, the initial hypothesis was that *P. dorsalis* would be more sensitive to drying conditions. A *desiccation experiment* was designed to determine if there were differences between species in rate of desiccation, tolerance to desiccation or amount of time until each species reached a physiologically critical threshold.

4. How are any differences in desiccation physiology reflected in habit use or other aspects of biology in the region of sympatry? The initial hypothesis was that *P. dorsalis* would be more intolerant of desiccation, unable to persist in xeric sites and found more often in more mesic microhabitats. The *cover object survey* was designed to sample both mesic and xeric habitats in cooler, wetter periods and in

warmer, drier periods so that any patterns of cover object usage influenced by desiccation physiology probably could be detected.

5. How different are these two populations in size distributions and growth allometries? Both species fall into Hairston's (1987) small *Plethodon* guild and have a quite substantial overlap in ranges of body sizes, a condition that normally results in asymmetrical competition and local exclusion (Hairston 1987). Sufficient differences in size distributions or allometries might have allowed enough niche separation to allow one species access to niches the other cannot access, or to preclude competition entirely (i.e., Jaeger et al. 1998). Salamanders collected during the *cover object survey* were measured for snout/vent length and mass to determine if there were significant differences in size or growth allometry that might help to explain the coexistence.

6. Do the species differ in levels of conspecific and interspecific aggressive behavior? The initial hypothesis was that *P. dorsalis* would be more aggressive, allowing it to largely exclude *P. cinereus* from the intrinsically more favorable mesic sites (presumably with more foraging opportunities). A *laboratory behavioral experiment* was designed to determine whether the species differed in levels of aggressive behavior, and therefore, presumably in competitive ability. Further, data from the *cover object survey* was analyzed for differences in cover object use that might reflect levels of aggressive behavior (i.e., a more aggressive species would be found less frequently in pairs and other social situations).

7. How are any differences in aggressive behavior related to the pattern expected to lead to coexistence under the classic Lotka-Voltera model? If

conspecific competition, as shown by levels of aggressive behavior, is stronger than interspecific competition, these interactions would provide an alternative explanation for broad sympatry, alternative to the more typical association between physiological sensitivity and increased aggressive behavior. The *laboratory behavior experiment* asked whether levels of conspecific aggression were higher than those of interspecific aggression. Such a finding would suggest that conspecific competition was stronger than interspecific competition.

8 and 9. Do the species differ in their ability to hold or invade cover objects in the field or laboratory? If so, how are these differences related to any differences in aggressive behavior? The dominant hypothesis in the literature is that differences in aggressive behavior predict ability to retain possession of better cover objects or to eject the resident from such objects. Thus, the initial hypothesis was that the more environmentally sensitive species (*P. dorsalis*) would be more aggressive and thus better able to preferentially obtain and maintain possession of better cover objects in the areas to which it is most physiologically adapted. A *field cover object experiment* was designed to examine the influence of size, species, and prior residency on the probability of successful invasion and the probability of the resident successfully maintaining ownership in such an area. A *laboratory cover object experiment* was designed to focus on the ability of each species, as an intruder and resident, to invade a cover object or to maintain residency of a cover object it already occupied when faced with an interspecific opponent. The results from the cover object experiments were compared with the results from the laboratory behavior experiment to address question 9.

Over the course of the research the focus was on the difference between the typical case in Plethodon (similar-sized species are allopatric, narrowly sympatric or ecologically segregated) and the syntopy of the two species in the current case. It was hoped that a difference in biology would reflect interesting differences in the underlying interactions.

Methods and Materials

Study area

All salamander sampling occurred in Hoosier National Forest in south-central Indiana. This area of Indiana was unglaciated and the terrain consists of dendritic networks of ridges and ravines resulting from erosion of a siltstone parent material (Lindsey, 1994). Differences in elevation of 60 meters from ridge top to ravine bottom are common. The different combinations of positions on the ridge and different aspects of the slopes create different habitats as evidenced by the plant communities. Hoosier National Forest consists mostly of the central mixed hardwoods communities. More mesic sites are dominated by maple (*Acer* spp.) and beech (*Fagus grandifolia*), while more xeric habitats are dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.). Pine plantations are scattered throughout the forest. These are typically several hectares in size and were planted primarily by the Civilian Conservation Corps as a reforestation project during the 1920s. The forest is entirely secondary growth due to clear cutting for timber and agriculture in the late 1800s. From its inception as a national forest and through the mid 1980s

the forest was harvested with even age management creating different aged former clear cuts typically several hectares in size (Van Kley et al. 1994).

Habitat plot survey: *What is the extent of overlap in habitat use across the range of more mesic and more xeric habitats?*

To determine the extent of sympatric coexistence and explore landscape level patterns of relative abundance, plot sampling was done in the springs of 1997 and 1998. Eighteen to twenty plots were randomly located along each of forty-five 100-m transects (a total of 894 plots). The length of the transects (100 m) was sufficient to disperse the plots and sample the range of conditions found within an area but short enough to stay within the stand type, position on the ridge, and aspect combination. Transects were run parallel to topographical lines to avoid changes in habitat associated with changes in position on the ridge. Transects in different aged stands were searched in a random order using a random number table. The starting point of each transect and the position of the plots were determined using a random number table. Transects were stratified by position on the ridge (top, middle, bottom), aspect (north (316-45 degrees azimuth), east (46-135 degrees), south (136-225 degrees), west (226-315 degrees)), and stand type. Stand types included pine plantations and three deciduous categories: young (15-25 yr after clear cutting), medium (26-60 yr), and mature (>60 yr). Age was determined from Hoosier National Forest timber stand data. Each plot was 2 sq m (i.e., 141 cm per side) in size and was delineated by a square PVC pipe frame.

A team of two people searched each plot. If a plot was unsearchable due to the base of a tree covering most of it or an immovable rock or log, the plot was placed on the other side of the transect. The percent of area in the plot covered by rocks or by branches that had fallen to the forest floor was visually estimated to provide a measure of cover object abundance. These cover objects were removed from the plot revealing any salamanders underneath. The leaf litter was then gathered to the middle of the plot revealing the duff underneath. This allowed any escape attempts of salamanders in the litter to be noticed. The litter was then sifted by hand to find salamanders that had remained in the litter. Captured salamanders were identified to species, measured from the tip of the snout to the anterior point of the vent (snout-vent length, SVL) and from the anterior point of the vent to the end of the tail, and then weighed using an Ohaus spring scale (±0.1 g). The salamanders were immediately released at the edge of the plot.

Analyses. To examine differences in abundance between species across the range of habitats in the plot sampling, a logit log-linear model was developed (Hutcheson and Sofroniou, 1999). Subsequently, the distributions of the two species across habitats and types of cover objects were compared with $\chi 2$ tests. Tests were performed using SPSS for Windows (Release 13.0.1).

Cover object survey: *Are there differences in microhabitat use (types of cover objects) that allow coexistence? How different are these two populations in size distributions and growth allometries?*

An additional study was initiated to examine possible differences in microhabitat usage. Cover objects were searched from November 2000 to June of 2001. By late May or early June conditions locally were typically warm and dry and *Plethodon* activity at the surface ceased or became rare. An effort was made to search every cover object in an area and to sample several habitats (i.e., different aspect and ridge positions in mature stands only) on any given day. The location of each salamander relative to others found under the same cover object was noted.

Soil moisture samples for the cover objects were taken by scooping a handful of soil and duff from directly under the salamander at the spot of capture, placing it in a plastic bag, and sealing the bag. These soil samples were taken back to the lab, weighed, dried to a constant weight in a drying oven and weighed again. The moisture measure was the percent weight a soil sample lost during drying.

Captured salamanders were placed in sealed plastic bags with some moist litter gathered nearby. Salamanders were taken to the lab. Each was anaesthetized with a small drop of Anbesol®, a commercial lidocaine solution, applied to the top of its head (methods from Alicia Mathis, personal communication). This facilitated accurate measurements while reducing stress. None of the salamanders died as a result of the lidocaine. After they were unresponsive, salamanders were blotted dry on a paper towel and their bladders were emptied by gently pressing on their lower abdomen. They were weighed on an Sartorius scale (±0.001 g) and SVL and tail

length were measured. They were identified to species and sexed using a variety of characters including pigmentation and folding of the cloaca and presence of testis or developing follicles when viewed backlit by a fiber optic light. Juvenile salamanders that had not yet begun to sexually differentiate in these characters were not sexed and are described as juvenile. Incidental mortality during a different project allowed direct examination of gonads thus providing a check of the accuracy of the externally sexing of adults, which was 100%. After measurement, salamanders were rinsed to remove any residual lidocaine, and placed in a clean 85 x 15 mm petri dish with fresh, saturated paper towels for substrate. These salamanders were later used for the laboratory behavior and cover object experiments, after which they were released in the area where they were captured.

Analyses. A logistic regression model was developed for the cover object survey data to examine any differences between species in their use of cover objects of different sizes or of those having different underlying moisture levels. The distributions of the two species (and the included demographic categories) across types of cover objects were compared separately with χ^2 tests and linear regressions since moisture levels covaried with the types of cover objects. The frequencies with which each species were found in groupings with conspecifics and with the other species were also examined with χ^2 tests. The relationship between cover object sizes and the numbers of salamanders captured underneath them were compared with an ANOVA. The average sizes of the two species, and their demographic subcategories, were compared with t-tests. Growth allometries were

compared with linear regressions on a log-log scale. Tests were performed using SPSS for Windows (Release 13.0.1**).**

Desiccation experiment: *How do the species differ in desiccation physiology?*

To examine possible differences in tolerance to drier habitats between the two species, salamanders were collected from Hoosier National Forest in the springs of 1999 and 2001. Salamanders were housed individually in 85 x 15 mm petri dishes, and kept at 19 degrees C with a 12-hour day/night cycle. To avoid potential confounding effects of food in the gut, salamanders were housed for five days without food before the trials. This allowed the salamanders to pass any recently ingested food (personal observation).

Both species were tested concurrently on each trial date, and individuals were randomly chosen from individually housed captive animals using a random number table. At the start of each trial, salamanders were blotted dry with paper towel and water in their bladders was expressed by pressing gently on their lower abdomen. This minimized differences between salamanders based on fullness of bladder or moistness of skin. Salamanders were weighed on a Sartorius scale (±0.001 g) and then suspended in small wire mesh (1 mm) cages. The cages were small enough to discourage any attempts to decrease water loss through behavioral means (e.g., curling into a ball). The cages were placed back on the scale every 10 minutes to provide a total weight of cage and salamander. To provide a measure of tolerance, salamanders were tested until they failed to respond to agitation of their

cage (80-193 mins). The change in weight during the trial resulted from water loss to the air and provides a measure of the rate of water loss.

Once a salamander failed to respond, the trial ended for that individual. The time was recorded and the salamander was removed from its cage, weighed again, and placed on a saturated paper towel in a clean petri dish to rehydrate. Salamanders that survived (69%) were later released in the area where they were captured.

Typically, salamanders that had ceased to respond to agitation were still breathing (maintaining gular movements). Thus, response to agitation provides a measure of physiological distress while reducing mortality associated with other measures of tolerance (e.g., Jaeger 1971).

Analyses. Regression was used to examine the rate of water loss (g/min) for the effects of year, species, and starting mass. Tolerance to water loss (as a percent of body mass) was compared with t-tests. An ANOVA was used to examine the effects of initial mass, year and species on time until no response. Tests were performed using SPSS for Windows (Release 13.0.1**).**

Laboratory behavior experiments: *Do the species differ in levels of conspecific and interspecific aggressive behavior? How are any such differences related to the pattern expected to lead to coexistence under the classic Lotka-Voltera model?*

Different levels of aggressive behavior might help explain the coexistence found in preliminary fieldwork. A laboratory study was developed to measure levels of aggressive behavior within and between the two species. Salamanders

were housed in a 19º C room with a single 20 watt light providing indirect light for 12 hours a day. Salamanders were held in a 85 x 15 mm petri dish with two layers of moist paper towel as substrate. The salamanders were placed into new dishes with new substrate every week as the old substrate became fouled. They were fed fruit flies (*Drosophila melanogaster*) ad-lib. three times per week. Extra flies were discarded when salamanders were placed in clean, new pens.

Using a random number table, salamanders were selected for use in the behavioral trials and size matched to within 2 mm SVL. Determination of resident and intruder was also by random number table. There were 26 *P. dorsalis* conspecific trials, 23 *P. cinereus* conspecific trials, 10 trials where *P. cinereus* was the resident and *P. dorsalis* was the intruder, and 17 trials were *P. dorsalis* was the resident and *P. cinereus* was the intruder. Initially, the number of planned trials were similar, but some pairings were excluded because of unusual circumstances such as the loss of a tail during a salamander's exploration of the arena or an excessive amount of handling to coax into the arena. Residents and intruders for a given trial were placed in identical 20 x 17 x 3 cm arenas with moist paper towel substrate and allowed five days to habituate to the arenas. This has been shown to be long enough for *Plethodon* to establish a territory that they will defend (Jaeger 1984). To increase the chance a salamander would find the arena worth defending, five fruit flies were blown in to each arena on day two and again on day four using a plastic tube. Trials took place five days after the salamanders were placed in the arena.

To start a trial, each salamander was gently prodded into a plastic tube and then gently prodded again to move out of the tube and under a 85 x 15 mm petri dish placed upside down on the substrate in the resident's arena. This method sought to reduce aberrant behavior potentially caused by excessive handling (Robert G. Jaeger personal communication). Salamanders were allowed five minutes to habituate under the petri dishes at which point the dishes were lifted and the arena top was gently placed back into place.

Salamanders were observed for fifteen minutes. Specific behaviors and the length of time each salamander engaged in each behavior were noted. The behaviors were classified as aggressive (all trunk raised, looking toward), submissive (flattened, looking away, and escape behaviors such as moving along the edge of the arena), and neutral (moving in a neutral direction, etc.). For conciseness and in accord with recent literature on *Plethodon* (e.g., Jaeger et al. 2002), aggressive displays are referred to as "aggression" and submissive ones as "submission." These behaviors and their interpretations have been previously described (Jaeger 1984, Nunes and Jaeger 1989, Jaeger et al. 2002).

Analyses. Amount of time spent in behavior categories (means in seconds) were compared with Mann-Whitney U tests using SPSS for Windows (Release 13.0.1**).**

Field cover object experiment: *Do the species differ in their ability to hold or invade cover objects in the field*?

A field experiment was designed to examine the effects of species, size, and prior residency on cover object invasion and on ability to maintain ownership.

Starting on May 12, 2001, cover objects were sampled for salamanders in the middle of a north-facing slope. This area was intentionally chosen as an area of high density to maximize rates of recapture and colonization. The initial sampling took place over three days with about 40 cover objects with salamanders under them located each day for a total of 114 initially occupied cover objects. Each cover object was assigned to either the control or the experimental group using a random number table. Salamanders found under cover objects in the experimental group were taken to the lab for detailed measurement and for use in laboratory behavior and cover object experiments, after which they were released in the area where they were captured. Salamanders under control cover objects were measured (snout/vent), identified to species, photographed to allow identification of individuals, and immediately returned to the cover object. Cover objects were resampled every ten days for a total of four times. Salamanders that were captured during resampling were measured, photographed, and returned to the cover object immediately, regardless of whether the cover object was control or experimental. The last resampling took place June 21-23.

Analyses. Rates of colonization and displacement (overall and by species) were compared using χ^2 tests. The effects of cover object size on these rates was examined with a t-test. An ANOVA was used to determine whether residency, species, or assignment to the control or experimental group differed with SVL. The pair-wise SVL differences between residents and intruders were calculated and included in the model as the dependent variable. The pattern of residency was coded into four categories (i.e., *P. dorsalis* to *P. dorsalis* transition, *P. dorsalis* to

P. cinereus transition, etc.) to test for effect of species as intruders and residents. Tests were performed using SPSS for Windows (Release 13.0.1**).**

Laboratory cover object experiment: *Do the species differ in their ability to hold or invade cover objects in the laboratory?*

A laboratory experiment examined the ability of each species to invade a cover object or to maintain residency under one. Sized-matched (<2 mm SVL difference) male *P. cinereus* and *P. dorsalis* were randomly paired together using a random number table and placed in separate, identical arenas in the laboratory. Salamanders were housed in a 19º C room with a single 20 watt light providing indirect light for 12 hours a day. Which salamander would be the resident was determined using a random number table. The arenas were plastic containers 16 x 30 x 8 cm in size. Since preliminary trials demonstrated that the arenas' lids did not slow moisture loss sufficiently, Saran Wrap® was secured under each arena lid with a rubber band to further reduce the loss of moisture. Arenas were stored in an order determined by a random number table with the constraint that no pairs were next to each other, eliminating the possibility of pairs that would face each other during the trial interacting before introduction. Each arena contained two cover objects made of gypsum based drywall, a high quality one and a poor quality one. The high quality cover object was larger, moister, and associated with food. The high quality cover object was 15 x 15 mm, while the poor one was 8 x 8 mm. The poor quality cover object was included to provide some refuge for any salamander excluded from the high quality cover object. Two layers of paper towels were

placed under each cover object. The paper towel under the high quality cover object was saturated with 50 ml of water. High quality cover objects were also soaked overnight to saturate with water and improve the moisture conditions associated with them. The paper towel under the poor cover object received 25 ml, which was enough to wet the towel, but not enough to saturate it. The paper towel under the high quality cover object was moistened as needed during trials to near saturation with an additional 25 ml of water. Poor cover objects received no additional water, but remained slightly damp due to the high humidity within the arena. Wingless fruit flies (*Drosophila melanogaster*) were blown in through a tube at the edge of the high quality cover object. The high quality cover object was placed with one edge in contact with one end of the container, and the poor quality cover object was placed with one edge in contact with the opposite end. The edges facing the middle of the container, and, therefore, the other cover object, were propped up with a marble to allow salamanders space under each cover object.

Salamanders were observed once daily just before the dark period of their light cycle. It was assumed that this would be before their normal nocturnal activity period and therefore reflect where they had spent the day hiding and resting. Their position within the arena was noted and categorized in one of three categories: associated with the high quality cover object, associated with the poor cover object, or in the neutral space between the two. Their position was further described by noting where they were in relation to the cover object. Salamanders were observed underneath, on top, along side, in back, on the wall above, and on the lid above a given cover object. The “in back” classification was used when a salamander was

observed in a groove formed between the back edge of the cover object and the wall of the arena. This area was small enough to only hold the width of one salamander and also provided access to the paper towel associated with the cover object. These observations were categorized as associated with the good cover object, the poor cover object, and the neutral area between them.

Two trials were performed in August of 2001. Initially, each salamander was observed in its home arena for six days in trial one and seven days in trial two. Each salamander was fed five fruit flies twice during the initial observation period. The flies were blown in through a tube to the back corner of the high quality cover object. After introduction of the intruder, salamander positions were observed as before, but no feeding or watering took place. To encourage drying, and therefore mimic the conditions in the forest between rain events, the Saran Wrap® plastic barrier was removed. This took place on the 5th day after the introduction of the intruder in the first trial, and on the 4th day in the second trial.

Exclusion was defined in several ways. It was considered exclusion if one salamander was associated with the high quality cover object, whether on top, underneath, etc., while the other was associated with the poor cover object. When both salamanders were associated with the high quality cover object, exclusion was scored if one salamander was underneath it while the other was found on top, on the wall or lid above, or in the groove behind the cover object. In these cases, the "excluded" salamander would not have been readily visible to the "resident", and therefore would have been less likely to elicit aggressive behavior from the resident. Many cases were ambiguous. For example, if one salamander was found

on top of the high quality cover object and another found on the wall above, it is unclear which one is excluding the other, or even if exclusion is taking place. To create a conservative measure of exclusion, these cases were scored "unclear".

Due to drying conditions within the arena the first trial ended ten days after the introduction of the intruder and five days after removal of the Saran Wrap® plastic barrier. The second trial ended six days after the introduction of the intruder and two days after the removal of the plastic barrier. The humidity in the trial room was not controlled and dryer weather during the second trial created stronger drying conditions in the trial room. In each trial, the substrate under the high quality cover object had dried to being merely damp and desiccation of the salamanders became a concern.

Analyses. A general linear model (GLM) was developed to test the effect of species on residency. Day was also included as an independent variable since drying mimicking field conditions might have shown an effect suggesting tolerance differences. Trial was also included, due to the moisture differences between trials. Tests were performed using SPSS for Windows (Release 13.0.1**).**

Results

What is the extent of overlap in habitat use across the range of more mesic and more xeric habitats?

In the plot search data, *P. cinereus* and *P. dorsalis* were found to coexist broadly and were found in all sites surveyed. Each species was found in each stand type studied (Table 1) and across the full range of aspects and from the top of the ridge to the bottom of the ravine (Table 2).

Logit log-linear model development proceeded by testing different models containing different possible variables and their interactions. The Newton-Raphson algorithm used by the software to estimate the model parameters failed to converge when testing the *P. dorsalis* data due to the number of plots with two or more *P. dorsalis* captures (eight plots with three individuals, one plot with four, and two plots with five). These categories were combined into a category of two or more captures, allowing the test to proceed. *P. cinereus* data did not need to be lumped like the *P. dorsalis* data, since there were only three plots with three individuals each and no plots with more than three. The model also failed to converge when aspect and position on ridge were treated separately. Therefore, these two variables were combined into one categorical variable, exposure (Table 2). Interactions and variables were eliminated and the difference between the fit of the old model and the fit of the new model were compared. If the new model was a statistically significantly poorer fit, the variable that created the difference in the model was retained, and the effects of other variables were tested. Model development proceeded until the removal of any remaining variables or interaction terms created a statistically significantly poorer fit (i.e., backwards stepwise regression).

The best-fit logit log-linear model describing the distribution of each species shows differences in distribution between the two species. *P. dorsalis* appeared to be the more environmentally sensitive species and was distributed significantly differently across different stands ($P<0.001$) and exposures ($P<0.001$). There was also a significant effect of year (Table 3, $P=0.006$). There was also a significant interaction effect of stand and year on *P. dorsalis* distributions (Table 4,

P=0.011). By contrast, none of these variables created significant differences in the distribution of *P. cinereus* (P=0.522, P=0.213 and P=0.325, respectively), and there were no statistically significant higher order effects.

Comparing the distributions of the two species with post hoc χ^2 tests supported the idea that each species was distributed significantly differently at the landscape level and that *P. dorsalis* was captured significantly less often in the drier year. *P. cinereus* capture rates were significantly less variable among different stand types ($\chi 2$= 16.2, df=3, P<0.001). *P. dorsalis* had a difference of 37.3% between the highest (45%) and lowest (7.7%) rate of occurrences (Table 1). In contrast, the difference between the most and least frequent occurrences of *P. cinereus* was 9.9%, from 15.4% to 25.3%. In the exposure data (Table 2), the largest difference in frequency of occurrence for *P. dorsalis* was 37.1%, from a low of 5% on the relatively dry west slopes to a high of 42.1% on the relatively moist north slopes. In contrast, the largest difference for *P. cinereus* was 11.3% ($\chi 2$= 17.9, df=5, P=0.003). *P. dorsalis* was captured in 24.5% of the plots in 1998 (double normal precipitation) compared to 15.1% in 1997 (normal precipitation), whereas the increase in plots containing *P. cinereus* was only 3.7% (Table 3, χ^2=2.086, df=1, P=0.148).

In summary, at a landscape level both species were found in all habitats sampled from the more xeric stands and aspects to the more mesic stands and aspects. *P. dorsalis* were captured more frequently in more mesic habitats and during the wetter year. In contrast, *P. cinereus* showed relatively little variation in capture frequency between more xeric and more mesic habitats and between years.

Are there differences in microhabitat use (types of cover objects) that allow coexistence?

Cover objects consisted primarily of rocks and fallen branches. The rocks were pieces of siltstone that tend to be relatively flat. The relevant branches fell from the larger trees that formed the canopy. There were a number of fallen logs throughout the areas examined, but only a small percentage of those were small enough to be turned. Of those, only a small number (<10) resulted in captures of salamanders. Thus, the woody debris under which salamanders were found consisted primarily of larger branches (average size was 13,086 cm^2).

Both the plot sampling and the cover object survey yielded data relevant to possible differences in cover objects where salamanders were found. In the plot sampling, both species were found underneath all cover types (rocks, branches, and litter). The ratios of captures under the different cover types did not differ significantly statistically between species (Table 5, χ^2=1.999, df=2, P=0.368). An average of about 75% of the captures were from leaf litter. *P. dorsalis* and *P. cinereus* capture rates under cover objects were similar with 11.1% and 10.6% respectively for branches, and 16.7% and 12.1% respectively for rocks. This does not suggest that litter was the preferred cover type since cover objects occupied an average of 4% of the plot area. The total cover object capture rate was 22.7% for *P. cinereus* and 27.8% for *P. dorsalis*, which suggests a preference for rocks and branches over litter, however there is no statistically significant difference between species (χ2= 1.508, df=1, P=0.219).

Captures under branches occurred on significantly moister substrate compared to rocks (logistic regression model; Figure 1, t= -19.778, df=214.018, P<0.001). Capture substrate under branches averaged 47.0% moisture by weight, while rock capture substrate averaged 29.2% moisture by weight. The confidence intervals associated with rocks were noticeably smaller than those associated with branches. There were no statistically significant differences between the species for cover object size (Figure 2, P=0.971) or moisture levels underneath the cover objects (Figure 1, Table 6, P=0.668). In the cover object survey, as in the plot sampling, there was no statistically significant difference in use of different cover object types between the species (Table 7, P=0.862).

Use of cover objects types in the survey was also not significantly different between matching genders and age of the two species (males χ^2=1.577, df=1, P=0.209, females χ^2=1.193, df=1, P=0.275, juveniles χ^2=1.124, df=1, P=0.289). Nor were there differences between matching genders and age of the two species for differences in size of cover object size or moisture levels underneath (logistic regression, males: P=0.621, P=0.425 respectively, Table 8; females: P=0.474, P=0.338 respectively, Table 9 ; juveniles: P=0.749, P=0.141 respectively, Table 10).

In summary, there were no statistically significant differences between the two species in use of different cover object types, in cover object size, or in moisture levels underneath cover objects. There also were no statistically significant differences in these variables between matched demographic categories (i.e., males v males) between species.

Do larger cover objects attract larger salamanders?

Lumping both species and rocks and branches together, there was no statistically significant effect of cover object size on SVL (linear regression; F=0.002, df=1, P=0.965, adj. R^2 = -0.002). Nor were the significant effects of cover object size when looking *P. dorsalis* captured under rocks (F=0.054, df=1, P=0.816, adj. R^2= -0.004) or branches (F=0.033, df=1, P=0.856, adj. R^2= -0.009). The same was true of *P. cinereus* captured under rocks (F=1.124, df=1, P=0.291, adj. R^2= -0.009) or branches (F=0.550, df=1, P=0.462, adj. R^2=0.001). These data provide no evidence that larger cover objects attract larger salamanders.

Do the two species differ in the frequencies with which they are found with conspecifics and with the other species (and, presumably, in their levels of conspecific or interspecific aggression)?

In the cover object survey, salamanders were considered occurring in a social setting if they were captured within 15 cm of each other, the standard previously used by others working with *Plethodon* (Jaeger 1979, Mathis 1989). Overall, 123 salamanders were found in social settings, accounting for 24.3% of all captures. The number of salamanders found in a group ranged from two to five. The difference between the two species of the rates of interspecific and conspecific social settings is statistically significant (χ^2, P<0.001, see Table 11 for statistical details). With *P. dorsalis* 25.2% of captures were in social settings with conspecific social situations occurring almost twice as often as interspecific social

settings, 64.9% compared to 35% respectively (Table 11). *P. cinereus* was captured in social settings 22.5% of the time with conspecific social settings much less frequent than interspecific social settings, 12.9% compared to 87% respectively. Most of the differences between observed and expected values came from the cells where each species was found in conspecific social settings and the cell where *P. cinereus* was found in interspecific social setting (Table 11). Specifically, *P. dorsalis* was found more often than expected in conspecific pairings, and *P. cinereus* was found more often than expected in interspecific pairings and less frequently than expected in conspecific pairings. There was no statistically significant difference in cover object size when comparing the numbers of salamanders captured underneath them (ANOVA; F=0.088, df=4, P=0.986).

How different are these two populations in size distributions and growth allometries?

In the cover object survey, on average, *P. cinereus* individuals were larger than *P. dorsalis*. Due to the logarithmic nature of the data, all tests were performed on log-transformed values for mass and SVL. The *P. dorsalis* SVL (mean=33.55 mm, sd=6.01052) was significantly smaller (Figure 3, t= -4.736, df=530, P<0.001) compared to *P. cinereus* (mean=36.44 mm, sd=5.79123). The mass of *P. dorsalis* (mean=0.51 g, sd=0.20491) also was significantly smaller (Figure 4, t= -4.012, df=420, P<0.001) compared to *P. cinereus* (mean=0.64 g, sd=0.23553). The same trend held when comparing only females (mass: t= -6.596, df=229, P<0.001; SVL: t= -6.394, df=184, P<0.001) and only males (mass: t= -4.377, df=174, P<0.001;

SVL: t= -4.336, df=204, P<0.001). Male *P. dorsalis* were not statistically significantly smaller (mass: t= -1.109, df=247.031, P=0.269; SVL: t= -0.944, df=287.153, P=0.346) than females in both SVL (male: mean=34.99 mm, sd=3.63077; females mean=35.49 mm, sd=4.17576) and mass (male: mean=0.54 g, sd=0.12232; females mean=0.58 g, sd=0.19547). Male *P. cinereus* were not statistically significantly smaller (mass: t= -3.718, df=109, P<0.001; SVL: t= -2.397, df=140, P=0.018) than females in both SVL (male: mean=37.28 mm, sd=3.56600; females mean=38.59 mm, sd=2.85474) and mass (male: mean=0.64 g, sd=0.15304; females mean=0.78 g, sd=0.19319).

While *P. cinereus* was significantly larger, it grew in an allometrically similar way to *P. dorsalis*: at each given length, both species had the same average mass, i.e., the linear regression lines on a log-log scale were essentially coincident (Figure 5).

How do the species differ in desiccation physiology?

Salamanders lost water at a constant rate during the trials. The slope of the resulting line for each salamander created a measure of rate of water loss (g/min). The regression for desiccation rate showed significant effects of year (P<0.001), species (P=0.002) and initial mass (P<0.001, Table 12, Figure 6). The effect of initial mass demonstrated that, as expected, water loss rates varied by size. Bigger salamanders lost water at a faster rate. The significant effect of year was a result of the differences in humidity between the years. The humidity was significantly higher in the laboratory in 2001, compared to 1999 (mean=83% sd=1.5 v 64%

sd=2.106, t=28.852, df=27, P<0.001) resulting in lower rates of water loss in 2001. *P. dorsalis* lost water at significantly faster rates compared to similarly sized *P. cinereus* in the same humidity environment. However this was evident only under the drier conditions of 1999 (Figure 6).

There was no statistically significant difference between species in the percent of water weight lost before they became unresponsive (t=0.179, df=27, P=0.859). *P. dorsalis* lost an average of 37.3% (N=13, sd=4.4) of its body weight while *P. cinereus* lost an average of 37.0% (N=16, sd=6.3). Time until no response showed significant effects (ANOVA) of initial mass (P<0.000) and year (P<0.000), but no significant effect of species (P=0.678). The significant effect of starting mass presumably resulted from smaller salamanders' larger surface/volume ratio. Their higher rate of water loss per unit mass resulted in reaching a critical threshold sooner relative to larger salamanders (data not shown). That is, while larger salamanders lost water at a faster rate, small salamanders lost it at a faster rate when factoring in differences in body size.

Do the species differ in levels of conspecific and interspecific aggressive behavior? Are *P. dorsalis* more aggressive?

Since time spent on one behavior cannot be spent on another, it was expected that aggression and submission would be negatively correlated. They were (for residents $r^2 = 0.608$, F=114.7, P<0.001; for intruders $r^2 = 0.587$, F=105.2, P<0.001). Consequently, statistics are reported only for aggressive behavior.

When combining all trials for both residents and intruders *P. cinereus* spent significantly more time in aggressive behaviors (Mann-Whitney U, P=0.026) and less time in submissive behaviors compared to *P. dorsalis*. This trend held for both residents and intruders: *P. cinereus* spent 25% and 42% more time in aggressive behaviors as residents and intruders, respectively, than did *P. dorsalis* (Figures 7 and 8). Similarly, *P. cinereus* spent 44% and 38% less time in submissive behaviors as residents and intruders, respectively, than did *P. dorsalis.* Thus, *P. cinereus* was, on average, more aggressive and less submissive than *P. dorsalis* across the range of trials, whether acting as intruders or residents.

Does increased aggression result in more wins (and presumably more frequent territory ownership)?

Previous studies using similar methods have defined a winner of a given trial as the individual, whether resident or intruder, the spent the most time in aggressive behavior as a pair-wise comparison. In the laboratory behavior experiments residents of both species exhibited more aggressive behavior than did the intruder in the majority of the trials when faced with a size-matched interspecific intruder (Table 13). *P. cinereus* residents won more interspecific compared to conspecific trials (χ^2=5.773, df=1, P=0.017). *P. dorsalis* residents also won slightly more interspecific as compared to conspecific trials, but this result was far from statistically significant (χ^2=0.273, df=1, P=0.601).

In summary, the laboratory behavior experiment demonstrated that *P. cinereus* was more aggressive than *P. dorsalis*, and this resulted in significantly

fewer interspecific wins by *P. dorsalis* intruders. Overall, each species as a resident won more frequently against interspecific intruders than against conspecific intruders.

Could higher levels of conspecific aggressive behavior compared to interspecific aggressive behavior explain coexistence?

Eight comparisons pertained to the relative strength of interspecific and conspecific competition (Table 14). Only three of the eight differed in the right direction to support the hypothesis that coexistence was maintained by stronger conspecific competition relative to interspecific competition. None were statistically significant.

Does the presence of residents deter invasion in the field?

In the field, 10 of the 44 experimental cover objects (original resident removed) were invaded, as were 12 of the 48 controls (original resident not removed). The difference was not significant (χ^2=0.040, df=1, P=0.841). Since there was no statistically difference between the colonization of experimental cover objects and the displacement of residents in the control cover objects, the data were compatible with the hypothesis that residency was not a deterrent to invasion. However, the high percentage of empty cover objects (i.e., control cover objects spontaneously abandoned and experimental cover objects with no new residents) may have swamped any effect of residents deterring intruders.

Is a larger size needed to overcome the effects of residency?

The SVL was not significantly different statistically between the control and the experimental group, showing that randomness did not inadvertently place larger or smaller salamanders into either group (Table 15, ANOVA: F=0.041, df=1, P=0.842). The differences in the sizes of SVL between residents and intruders was significantly different depending on which species were involved in the transition (F=4.409, df=3, P=0.016). There was only one *P. dorsalis-P. dorsalis* transition. *P. cinereus-P.cinereus* transitions averaged .36 mm meaning that on average, the residents were less than a millimeter larger than intruders (N=11, sd=5.500). By contrast, *P. dorsalis* residents averaged 6.56 mm (N=9, sd=7.126) smaller than *P. cinereus* intruders into their cover objects. *P. dorsalis* intruders averaged 7.67 mm smaller than the *P. cinereus* residents they replaced (N=7, sd=7.763). This pattern was true whether looking at control or experimental cover objects (Table 16). For comparison, the average for all *P. dorsalis* in the cover object survey was 2.89 mm smaller than that for *P. cinereus.*

Do the species differ in their ability to hold or invade cover objects in the field?

In the field experiment, the invasion rates for experimental cover objects where the resident had been removed were not statistically significantly different between species (χ^2=7.403, df=1, P=0.116, Table 17). However, *P. cinereus* was significantly more likely to colonize control cover objects compared to *P. dorsalis* (χ^2 P=3.941, df=1, P=0.041). The numbers in Table 16 are larger than the numbers

reported above since once a cover object had been invaded the invader was subsequently considered a resident. The appearance of new salamanders in further samplings then counted as invaders. The ratios for each species are similar between experimental and control cover objects (15/7 v 8/5) so it is possible the lack of significance in the experimental data is the result smaller sample size reducing statistical power.

Are larger cover objects colonized or invaded at a higher rate?

In the field experiment, there was no significant difference in size between cover objects where new residents (mean=892 cm^2, sd=1145) were captured and those where no new salamanders (mean=832 cm^2, sd=688) were captured (t = -0.165, dF=57, P=0.869). The different categories of control cover objects (empty, intruders, and original residents) were not statistically significantly different in size (Kruskal-Wallis, χ^2=5.567, df=2, P=0.062), although the low P-value was suggestive.

Did disturbance shift the species ratios in recaptures?

Sampling of previously undisturbed cover objects during the second recheck on June 3rd 2001 (initial sampling started May 12th) produced a capture ratio of 5 *P. dorsalis* to 8 *P. cinereus.* The 5/8 ratio of captures under these undisturbed cover objects was very similar to the recapture 12/23 ratio for all recaptures (χ^2=0.072, df=1, P=0.788).

Does relative abundance shift seasonally?

The June ratio of 17/31 (*P. dorsalis*/*P. cinereus*) from these two samples combined was significantly lower than the May 12-14 capture ratio of 70/60 (χ^2=4.765, df=1, P<0.04). These data underestimated the magnitude of the seasonal shift in relative species abundances: the May and June samples were collected on a north-facing slope where earlier *P. dorsalis* had outnumbered *P. cinereus* based on both the plot and the cover object sampling data. Combining sample data from the cover object survey from a range of habitats in November, February and April with the data from the cover object experiment during May and June showed a strong seasonal shift in capture ratios (Table 18, χ^2=25.343, dF=4, P<0.001).

Do the species differ in their ability to hold or invade cover objects in the laboratory? Can *P. dorsalis* better maintain residency?

When living alone in the laboratory, individuals of both species were observed in association with the high quality cover object far more frequently (84% for *P. cinereus*, 77% for *P. dorsalis*) than with the poor cover object or the neutral area between them (Table 19). There was no significant difference between the species (χ^2=1.890, df=2, P=0.389).

After the introduction, about 50% of the observations recorded no clear case of exclusion whether the original resident was *P. dorsalis* or *P. cinereus* (47.1% v 53.4%, Table 20). In the clear cases, *P. dorsalis* excluded *P. cinereus* from the higher quality cover objects more frequently than *P. cinereus* excluded *P. dorsalis*

both as a resident and as an intruder (Table 20). The effect was stronger when *P. dorsalis* was the resident.

There were significant effects (GLM) on ownership of day ($F=3.218$, $df=9$, $P=0.001$), species ($F=17.775$, $df=1$, $P<0.001$) and trial ($F=4.064$, $df=1$, $P=0.044$). While day is significant, it reflects variation between days and not a positive or negative trend in exclusion between species. The difference between the two species reflected the higher rates of exclusion of *P. cinereus* by *P. dorsalis* both as a resident and an intruder. The suggestive difference between the trials reflected the differences between the amounts of exclusion by residents compared to the amount of exclusion by intruders (Table 20). The reasons for the difference between trials was unknown, but might have resulted from the dryer conditions (as evidenced by the faster rate of substrate drying) in the room at the time. *P. cinereus* appeared to be slightly better at holding the cover object in trial 2 compared to trial 1, but *P. dorsalis* was still able to exclude *P. cinereus* at higher rates.

Discussion

What is the extent of overlap in habitat use across the range of mesic and more xeric habitats?

Both species coexist broadly at a landscape level. Both were found in all stand types sampled, across the full range of aspects, and from the top of the ridge to the bottom of the ravine. However, *P. dorsalis* was captured at significantly different rates across different stand types and across different aspects and ridge positions (exposure). Its distribution pattern suggested sensitivity to more xeric

habitats, as *P. dorsalis* was less common in young deciduous and pine stands and less common on west and south facing slopes (v east and north). Further, *P. dorsalis* was captured significantly less frequently during 1997, a year with normal precipitation, than during 1998, a year with twice the normal precipitation. By contrast, *P. cinereus* was not captured at rates that were statistically different between years or across stand types and different exposures. This suggested that *P. cinereus* was more tolerant of xeric conditions compared to *P. dorsalis*.

The cover object sampling data and the field cover object experiment data also supported a difference in environmental sensitivity between the two species. There was a significant seasonal shift in relative abundance from predominantly *P. dorsalis* to *P. cinereus*.

Interestingly, *P. dorsalis* were found at a relatively high frequency at the top of the ridge, a frequency similar to the frequency at the bottom of the ravine. Ravine bottoms contained the rocky streams considered their primary habitat by Thurow (1955). One might have thought that salamander habitat at the top of the ridge would have been significantly drier. However, the soils at the tops of the ridges were derived from siltstone and had a large amount of clay. Water pools readily and infiltrates poorly into these soils (Van Kley et al. 1994) during the part of the year when salamanders are active on the surface. The lack of infiltration probably kept the ridge top habitats relatively more mesic than the west and south slopes.

Are there differences in microhabitat use (types of cover objects) that allow coexistence?

Cover objects comprise about 4% of the forest floor but were responsible for 25% of the captures during the plot sampling. This suggested that cover objects provide better habitat than litter for salamanders, a conclusion that was supported by the numerous previous studies of *Plethodon* showing aggressive behavior used in cover object defense (for a review see Mathis et al. 1995).

However, despite the importance of cover objects compared to litter and the differences between cover object types in moisture levels, there were no statistically significant differences between species in types of cover objects used in either the plot sampling or the cover object searches. Nor were there statistically significant differences between species or between matched demographic classes between species in cover object size or in moisture levels. This contrasts with both the landscape distribution and the water loss data that demonstrated differences between these two species in south-central Indiana.

The lack of differences at the microhabitat level suggests a certain level of homogeneity in cover object attributes at a smaller scale. It contrasts with Mathis' (1990) work in a more open canopy environment showing larger salamanders more frequently using larger cover objects. Gabor (1995) tested the Mathis hypothesis with salamanders from a different area and found no relationship between size of salamander and size of cover object. Gabor explained the difference as a result of the closed canopy providing enough environmental buffering to minimize differences between cover objects on a small scale. In the current study, the lack of

significant differences between species also holds true for differences between species in matched demographic classes (male, female, juvenile). This suggests that Gabor's environmental buffering hypothesis also applies to the populations studied here.

Are any differences in desiccation physiology reflected in habit use? Does the desiccation physiology differ in a way that could explain the coexistence?

The field data that supported the hypothesis that *P. dorsalis* was more sensitive to xeric conditions was also supported by laboratory water loss rates. While both species tolerated the same amount of water loss as a percentage of body mass, *P. dorsalis* lost water at a significantly faster rate than did *P. cinereus* in the same humidity environment.

There was a possibility that difference in allometric scaling could account for the differences in water loss rates. That is, salamanders of the same length could have significantly different masses thereby giving them different surface area to volume ratios, which would have explained the different rates as a result of physics rather than the properties of the skin of the two species. Instead, the two species had strikingly similar mass:SVL allometries, which suggested that the difference in rate was not the result of allometric differences in growth.

Because the rate of water loss varied inversely with humidity, it was possible that the slope for *P. dorsalis* in 2001 was an artifact of larger individuals having been tested on more humid days. This was not the case as all trials in a

given year were run simultaneously on the same day. Here, too, the significant effect of year was a result of the differences in humidity between the years.

Distribution, desiccation and the *P. dorsalis* dilemma.

It is important to remember that in this case, unlike most of the other cases that have been studied in *Plethodon*, these two species coexist sympatricly over a range of several thousand square miles. While some other cases may be considered sympatric at a landscape level (e.g., Jaeger 1971, Marshal et al. 2004), the two species in such cases do not overlap significantly in microhabitat usage. The current study found syntopic coexistence, existing side by side in the same microhabitats, over a range of at least several hundred square miles and across the full range of habitats and types of cover objects examined. This makes the *P. cinereus* - *P. dorsalis* case appear unique among *Plethodon.*

P. dorsalis was the more environmentally sensitive species. It was captured more frequently on east and north facing slopes, in mature stands and during a wetter year. They were also more frequently captured at cooler, wetter times of the year. Further, *P. dorsalis* had a greater rate of water loss in the laboratory. Conversely, *P. cinereus* was distributed more evenly across stands, exposures and years and had a lower rate of water loss in the laboratory. The greater robustness of *P. cinereus* suggests several ways that *P. cinereus* can coexist with *P. dorsalis*, i.e., several ways in which it should have access to resources from which *P. dorsalis* is largely excluded.

But these data leave unresolved the question of how *P. dorsalis* can coexist with *P. cinereus*. Ideas that explain community assembly from species that are competitively equivalent (e.g., Hubbell 2001, Volkov et al. 2003) might have seemed tempting for this interaction at this point in the analysis. However, the fact that each species reacted aggressively to the other seemed to suggest that they compete for essential resources (Brown 1964). Thus, a closer examination of the size differences, behavioral interactions and cover object results was needed before neutrality or equivalency might have seemed reasonable.

How different are these two populations in size distributions?

P. cinereus was statistically significantly larger than *P. dorsalis* for both snout/vent length and mass. Not only was *P. dorsalis* smaller on average, but also the largest individuals were typically *P. cinereus*, meaning that there was no size class *P. dorsalis* could grow to and escape competition for food from *P. cinereus* by exploiting niches unavailable to *P. cinereus*. Thus the size differences were in the opposite direction from those that may have explained the persistence of *P. dorsalis* in the presence of *P. cinereus*. Instead, it suggested that *P. cinereus* could eat all prey sizes available to *P. dorsalis*, plus larger prey sizes as they grow past the sizes typical of *P. dorsalis*.

Apparent character displacement in feeding apparatus has been documented from a narrow band of sympatry along the margin of the contiguously allopatric ranges of *P. cinereus* and *P. hoffmani* (Adams and Rohlf 2000). *P. cinereus* diverged to specialized more on smaller prey types whereas *P. hoffmani* became

somewhat more specialized on larger prey types. At first glance, similar changes unless extreme would not seem to explain how *P. dorsalis* can persist in competition with *P. cinereus*. Since *P. cinereus* is larger than *P. dorsalis,* a shift in its diet towards smaller prey would seem to increase dietary overlap. Conversely, a shift for *P. dorsalis* toward either smaller or larger prey would not seem to remove it from dietary similarity with *P. cinereus*.

Do the species differ in levels of conspecific and interspecific aggressive behavior?

Behavioral trials that measure levels of aggressive behavior have been used extensively in the past to measure relative strength of competition (e.g., Jeager et al. 1998, Nishikawa 1985) and predict the eventual owner of a cover object (Jaeger 1984). Although *P. dorsalis* is physiologically more sensitive, it could persist in the same habitats as *P. cinereus*, unlike *P. shenandoah* (Wrobel et al. 1980), if it were more aggressive than *P. cinereus*. Lotka-Voltera competition models would also predict coexistence if conspecific competition were stronger than interspecific competition. The behavioral experiments in the lab sought to test these hypotheses by comparing levels of aggressive, submissive, and neutral behaviors in both interspecific and conspecific interactions.

In many measures, *P. cinereus* (rather than *P. dorsalis*) appeared to be more aggressive. *P. cinereus* spent significantly more time in aggressive behaviors across all trials and lumping both residents and intruders. This difference was found for both residents and intruders. Conclusions based on previous literature (Wrobel et

al. 1980, Jaeger 1984, Marvin 1998, Marshall et al. 2004) suggested that *P. dorsalis* intruders would rarely be able to invade cover objects held by *P. cinereus* residents and that *P. cinereus* individuals might be able to overcome the effects of residency and invade cover objects occupied by *P. dorsalis*.

How are any differences in aggressive behavior related to the pattern expected to lead to coexistence under the classic Lotka-Voltera model?

Given the apparently higher levels of aggressive behavior in *P. cinereus* it was useful to ask how many trials were "won" by a given species where an individual spending more time in aggressive behaviors than its opponent won a trial. If the resident spent more time in aggressive behaviors than the intruder, the resident won. If the intruder spent more time in aggressive behaviors, the intruder won. *P. cinereus* residents won significantly more interspecific compared to conspecific trials. *P. dorsalis* residents also won more interspecific compared to conspecific trials, but this result was far from statistically significant.

Thus, *P. cinereus* was the more aggressive species and had a statistically significant number of "wins" in pair-wise comparisons. However, the key feature of these results is that resident *P. cinereus* were more successful in winning interspecific as compared to conspecific trials. This is precisely the opposite of the pattern for *P. cinereus* that would have been required to allow *P. dorsalis* to coexist with *P. cinereus* under the classic Lotka-Voltera model.

Eight comparisons of means together also addressed the idea that the coexistence might have been mediated by stronger conspecific competition relative

to interspecific competition. None of these comparisons were statistically significant and several were in the wrong direction to support this hypothesis. Thus, these laboratory behavior experiments provided no evidence that stronger conspecific competition relative to interspecific competition allowed the coexistence between these two species.

Do the two species differ in the frequencies with which they are found with conspecifics and with the other species (and, presumably, in their levels of conspecific or interspecific aggression)?

P. cinereus had higher levels of aggression as measured in the lab and was hyperdispersed in the field, rarely being found with conspecifics. By comparison, *P. dorsalis* had lower levels of aggression in the lab found together with conspecifics in the field more often than expected by chance. Further, although *P. cinereus* in the laboratory were even more successful in winning interspecific than conspecific contests, individual *P. cinereus* were found with *P. dorsalis* more often than expected by chance. The hyperdispersion of *P. cinereus* may have left unoccupied space that could be used by *P. dorsalis* despite its smaller size, lower levels of aggression, and greater environmental sensitivity.

Do the species differ in their ability to hold or invade cover objects in the field or laboratory? If so, how are these differences related to any differences in aggressive behavior?

In the laboratory cover object experiment, both species when alone occupied the higher quality cover object significantly more often than the lower quality cover object. Whether a resident or an intruder in interspecific pairings, *P. dorsalis* excluded *P. cinereus* at significant rates. Further, the ability of *P. dorsalis* to both maintain residency and displace *P. cinereus* residents suggested that even if *P. cinereus* were genuinely more aggressive, *P. dorsalis* could have persisted in the field due to its superior ability to invade cover objects and maintain it's ownership of them. This was consistent with the cover object survey data showing the *P. cinereus* is found together with *P. dorsalis* more frequently than expected and less frequent with conspecifics than expected.

This was interesting given the higher levels of aggressive behaviors found in *P. cinereus*, and suggested that levels of aggressive behavior did not map directly onto eventual cover object ownership. In contrast, prior work has considered the more aggressive species as the probable winner in the competition for a cover object. Wrobel et al. (1980) linked higher levels of aggression to the competitive superiority of *P. cinereus* over *P. shenandoah*. Similarly, *P. glutinosus* had higher levels of aggression in the laboratory relative to *P. kentucki*. This appeared to result in a pattern in the field where *P. kentucki* was relegated to smaller cover objects (Marvin 1998). *P. glutinosus* also had higher levels of aggression in the laboratory relative to *P. petraeus*. The higher levels of aggression appeared to translate into a pattern in the field where *P. petraeus* was relegated to patches of habitat unsuitable for *P. glutinosus* (Marshal et al. 2004).

At least three factors help explain the ability of *P. dorsalis* to occupy cover objects in the laboratory and, perhaps, in the field, despite competition from the larger, more aggressive *P. cinereus.* One is the greater tolerance of *P. dorsalis* for both conspecific and interspecific neighbors under cover objects in the field. A second is, paradoxically, the greater physiological tolerance of *P. cinereus.* As classically pointed out by Brown (1964), the effort expended in defending a resource should depend on the cost of not having that resource. The lower sensitivity to dehydration of *P. cinereus* may have made the cover objects in the laboratory and field less important to it than to *P. dorsalis.* Finally, at least in theory a less aggressive individual can sometimes secure a small piece of territory from a more aggressive individual by repeatedly seeking the same small area, thereby raising the cost of that incremental piece of territory to a level that exceeds its value to the more aggressive individual (Stamps and Krishnan 2001). This is made more plausible for *P. dorsalis* by its greater tolerance for close neighbors in the field, a finding that clearly shows that the space under at least some cover objects is indeed divisible. Another way of stating these factors would be to say that *P. dorsalis* occurs above ground disproportionately in moister habitats and at moister times of the year where food is probably more accessible and defense of a large territory is consequently less salient. In contrast, *P. cinereus* is much more relatively abundant in drier habitats and persists in above ground activity later in the spring when conditions become somewhat hotter and drier when its hyperdispersion may be more important in keeping access to sufficient food and an array of cover objects. Thus, *P. dorsalis* might be viewed as a specialist on the

richest resource situations, a species whose strategies include increased social tolerance, more success in obtaining and holding space under a cover object, and quicker retreat in the face of adverse conditions. In this frame, *P. cinereus* would be seen as more of a generalist and their coexistence would fit the classic model of a specialist persisting in a rich but limited part of the resource space of a generalist. This provides a strong contrast to the other cases studied in *Plethodon*, most or all of which seem to be of partial exclusion of a less dominant species from the richest part of the habitat.

Summary

Previous work on *Plethodon* has repeatedly shown asymmetric competition resulting in exclusion whether on the scale of different sizes of cover objects, of habitat patches, or of hectares or landscapes. Unlike previously studied pairs of similar-sized *Plethodon*, *P. cinereus* and *P. dorsalis,* coexist broadly and syntopically across the range of mesic and xeric habitats. While *P. dorsalis* was relatively more abundant in damp ravines and on heavily wooded hillsides (i.e., north and east facing slopes), there appeared to be no habitat or microhabitat (cover object) segregation of the two species.

The landscape patterns of relative abundance suggested that *P. dorsalis* was more environmentally sensitive. This was supported by other field data that demonstrated a shift in relative abundance to increasingly favor *P. cinereus* as the spring warmed and dried. It was also supported by the water loss data in the lab, which demonstrated that *P. dorsalis* lose water at significantly higher rates

compared to *P. cinereus*. Although their growth allometries were essentially identical, *P. cinereus* was significantly larger on average. This suggested that *P. cinereus* might frequently be able to prey on larger prey than those taken by *P. dorsalis*.

In contrast to much of the previous *Plethodon* work showing more aggressive species and individuals more likely to win cover objects, *P. dorsalis* was less aggressive in standard tests but was better able to invade and hold cover objects both a resident and intruder. And in the field *P. dorsalis* co-occurred with *P. cinereus* more frequently than expected by chance, whereas *P. cinereus* co-occurred with conspecifics less frequently than expected by chance. The better ability of *P. dorsalis* to hold cover objects and the hyperdispersion of *P. cinereus* in the field offer a framework for explaining how a smaller, less aggressive, more environmentally sensitive species can persist when in competition with a larger, more aggressive, more environmentally robust species.

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Table 1. Percent of plots containing each species in each stand type. Column totals are total number of plots in each category. The differences between species are significant ($\chi 2$= 16.2, df=3, P<0.001).

	stand			
	mature	medium	young	pine
P. dorsalis	26.6%	45.0%	7.7%	18.8%
P. cinereus	25.3%	25.0%	19.6%	15.4%
Plots N	466	40	271	117

Table 2. Percent of plots containing each species in each exposure class. Column totals are total number of plots in each category. The differences between species are significant ($\chi 2$= 17.9, df=5, P=0.003).

	exposure					
	west	south	top of ridge	ravine bottom	north	east
P. dorsalis	5.0%	8.8%	20.5%	18.5%	42.1%	26.3%
P. cinereus	25.0%	20.6%	17.1%	25.5%	28.4%	21.1%
Plots N	60	68	293	302	95	76

Table 3. Percent of plots containing each species for each year. Column totals are total number of plots in each category. The differences between species are not significant ($\chi 2$= 2.086, df=1, P=0.148).

	year	
Species	1997	1998
P. dorsalis	15.1%	24.5%
P. cinereus	20.1%	23.8%
Plots N	364	530

Table 4. Percentage of plots containing *P. dorsalis* in each stand type and year. Column totals are total number of plots in each category. The interaction was significant (logit log-linear model P=0.011).

Year	mature	medium	young	Pine
1997	20.0%	0	6.0%	10.8%
1998	32.0%	45.5%	9.0%	22.5%
Plots N	466	40	271	117

Table 5. Counts of salamanders associated with each type of cover object used by each species in the plot sampling. Numbers are counts of salamanders found associated with each cover type. There was no statistically significant difference between the two species (χ2= 1.999, df=2, P=0.368).

	cover object type		
species	rocks	branches	litter
P. dorsalis	36	24	155
P. cinereus	25	22	160

Table 6. Logistic regression model for differences between species in size of cover objects and percent moisture underneath cover objects in the cover object survey where salamanders were captured.

variable	B	S.E.	df	sig.	Exp(B)
size of cover	0.000	0.000	1	0.971	1.000
percent moisture	0.455	1.060	1	0.668	1.576
constant	-1.115	0.378	1	0.003	0.328

Table 7. Type of cover object used by each species in the cover object survey. There was no statistically significant difference between the two species (χ^2=0.030, df=1, P=0.862).

	cover object type	
species	rocks	branches
P. dorsalis	256	108
P. cinereus	119	52

Table 8. Logistic regression model for differences between males of each species in size of cover objects and percent moisture underneath cover objects in the cover object survey where salamanders were captured.

variable	B	S.E.	df	sig.	Exp(B)
size of cover	0.000	0.000	1	0.621	1.000
percent moisture	1.292	1.621	1	0.425	3.640
constant	-1.103	0.573	1	0.054	0.332

Table 9. Logistic regression model for differences between females of each species in size of cover objects and percent moisture underneath cover objects in the cover object survey where salamanders were captured.

variable	B	S.E.	df	sig.	Exp(B)
size of cover	0.000	0.000	1	0.474	1.000
percent moisture	-1.805	1.885	1	0.338	0.164
constant	-0.602	0.646	1	0.351	0.547

Table 10. Logistic regression model for differences between juveniles of each species in size of cover objects and percent moisture underneath cover objects in the cover object survey where salamanders were captured.

variable	B	S.E.	df	sig.	Exp(B)
size of cover object	0.000	0.000	1	0.749	1.000
percent moisture	4.691	3.185	1	0.141	108.975
constant	-2.862	1.185	1	0.016	0.057

Table 11. Numbers of each species found and expected numbers used to calculate the χ^2 values in conspecific and interspecific social situations in the cover object survey (χ^2=24.174, df=3, P<0.001). Asterisks are cells with χ^2 values significant at 1 degree of freedom and the P=0.005 level (larger than 3.84). These observed values differ significantly from expected values.

	species					
	P. dorsalis			*P. cinereus*		
social setting	count	expected	χ^2	count	expected	χ^2
alone	247	255	0.037215	128	128	0.074209
conspecific	50*	36	5.47756	4*	18	10.92271
interspecific	26	36	2.234457	26*	18	4.455691
found with both species	8	10	0.396449	7	5	0.790552

Table 12. GLM of the desiccation rate in the laboratory as a function of year and species. Starting mass is treated as a covariate (adjusted R-squared = 0.649). The rate differed significantly between species, between years, and with starting mass. Years was significantly different due to the different humidity levels in the testing room.

source	Type III SOS	df	mean square	F	sig.
corrected model	4.081	3	1.360	18.288	0.000
intercept	2.189	1	2.189	29.426	0.000
Year	1.683	1	1.683	22.621	0.000
Mass	2.547	1	2.547	34.246	0.000
species	.896	1	.896	12.049	0.002

Table 13. Winners in the paired laboratory behavior experiment. Winners were defined as the individual that spent the most time in aggressive behavior.

treatment		winner	
resident	intruder	resident	intruder
P. dorsalis	*P. cinereus*	11	6
P. cinereus	*P. dorsalis*	9	1
P. dorsalis	*P. dorsalis*	12	14
P. cinereus	*P. cinereus*	13	10

Table 14. Relative strengths of interspecific and conspecific competition. "Yes" (or "No") indicate a difference between categories in the direction that would support (or would not) the idea that conspecific competition is greater than interspecific competition (mean in seconds are given in parenthesis). NS=not statistically significant. P-values are from Mann Whitney U tests.

Aggressive behavior		P-value
Are *P. dorsalis* residents more aggressive to conspecific intruders than to *P. cinereus* intruders? (344 to 345)	no, NS	1.000
Are *P. dorsalis* intruders more aggressive to conspecific residents than to *P. cinereus* residents? (281 to186)	yes, NS	0.639
Are *P. cinereus* residents more aggressive to conspecific intruders than to *P. dorsalis* intruders? (434 to 410)	yes, NS	0.428
Are *P. cinereus* intruders more aggressive to conspecific residents than to *P. dorsalis* residents? (329 to 335)	no, NS	0.588
Submissive behavior		
Are *P. dorsalis* residents less submissive to conspecific intruders than to *P. cinereus* intruders? (409 to 287)	no, NS	0.150
Are *P. dorsalis* intruders less submissive to conspecific residents than to *P. cinereus* residents? (462 to 641)	yes, NS	0.191
Are *P. cinereus* residents less submissive to conspecific intruders than to *P. dorsalis* intruders? (247 to 215)	no, NS	0.984
Are *P. cinereus* intruders less submissive to conspecific residents than to *P. dorsalis* residents? (400 to 390)	no, NS	0.859

Table 15. GLM table for pair-wise snout/vent length as the dependent variable in the cover object field experiment (adjusted R-squared=0.425). Treatment compares SVL between experimental cover objects where the original resident was removed, and control cover objects where the original resident was returned to the cover object. Residency compares the SVL of the original residents of the cover objects compared to intruders (i.e., captures of new individuals in subsequent sampling).

Source	Type III SOS	df	mean square	F	sig.
corrected model	743.593	6	123.932	2.468	0.060
Intercept	2.377	1	2.377	0.047	0.830
Transition	664.326	3	221.442	4.409	0.016
Treatment	2.050	1	2.050	0.041	0.842
transition*treatment	4.537	2	2.269	0.045	0.956

Table 16. Snout/vent length of residents minus snout/vent length of intruders. Control cover objects had the original resident returned after identification, while experimental cover objects had the original resident removed. *P. dorsalis* intruders were smaller on average than the *P. cinereus* residents they replaced, while the *P. cinereus* intruders which were larger on average than the *P. dorsalis* they replaced. This difference was statistically significant (post hoc t= -3.658, df=13, P=0.003).

	treatment					
transition	control			experimental		
	mean	N	sd	mean	N	sd
P. dorsalis to *P. dorsalis*	.	1	.	.	0	.
P. cinereus to *P. cinereus*	0.14	7	2.410	0.75	4	9.430
P. dorsalis to *P. cinereus*	-6.25	4	6.449	-6.80	5	8.379
P. cinereus to *P. dorsalis*	6.50	2	3.536	8.25	4	9.743

Table 17. Number of intruders and residents by species for each treatment. *P. cinereus* colonized control (resident not removed) cover objects significantly more often compared to *P. dorsalis* (χ2=3.941, df=1, P=0.041). There was no statistically significant difference in invasion rates between species for experimental cover objects (χ^2=0.739, df=1, P=0.390).

treatment	species	residents	intruders	total
control	*P. dorsalis*	35	7	42
	P. cinereus	27	15	42
	total	62	22	84
experimental	*P. dorsalis*	35	5	40
	P. cinereus	33	8	41
	total	68	13	81

Table 18. Capture ratios by month. May and June samples were from north slopes only (χ^2=25.343, df=4, P<0.001).

	Nov.	Feb.	April	May	June
P. dorsalis	65%	72%	74%	54%	38%
P. cinereus	35%	28%	26%	46%	62%
Total N	161	88	399	130	13

Table 19. Raw numbers and percentages of observations of salamanders and their association with cover objects prior to the introduction of an intruder. Numbers are all observations for each salamander total.

cover object association	species			
	P. dorsalis		*P. cinereus*	
	N	%	N	%
high quality	267	79	289	82
poor	42	12	43	12
neutral	28	8	20	6

Table 20. Exclusion in the cover object experiment. The percentages are based on the total number of observations individuals were observed excluding their opponent. Trial one had 33 pairings and 10 observations of each pairing. Trial two had 30 pairings and 6 observations of each pairing. The differences between species were significant (nominal regression $P<0.000$).

species of resident	winner	percent of observations		
		trial 1	trial 2	average
P. dorsalis	*P. dorsalis*	39.0	32.3	36.8
	P. cinereus	13.8	20.8	16.1
	unclear	47.2	46.9	47.1
P. cinereus	*P. cinereus*	18.4	19.0	18.6
	P. dorsalis	30.1	23.8	28.0
	unclear	51.6	57.1	53.4

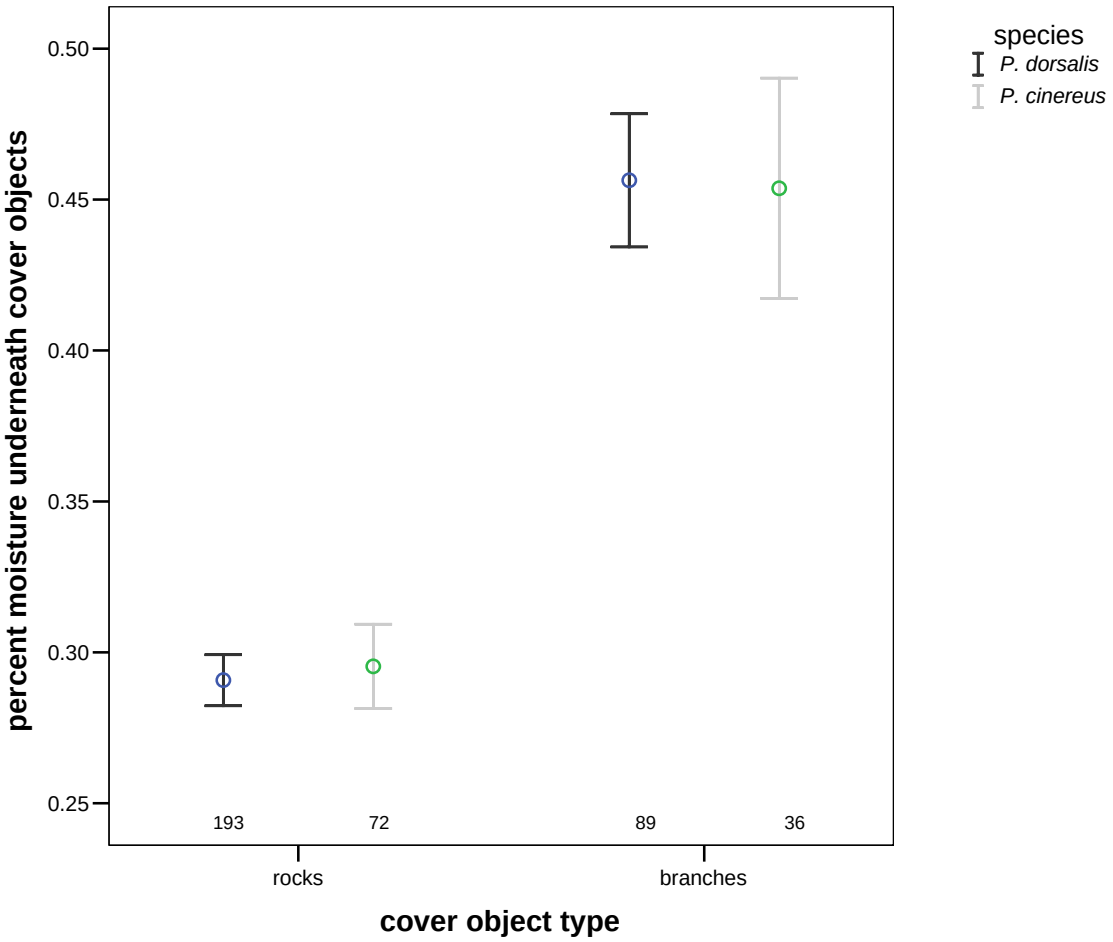

Figure 1. Mean moisture levels underneath the rocks and branches where each species was captured. Y-axis is the percent of weight removed from soil samples when dried to a constant temperature. The error bars represent 95% confidence intervals. Numbers are samples sizes for each species.

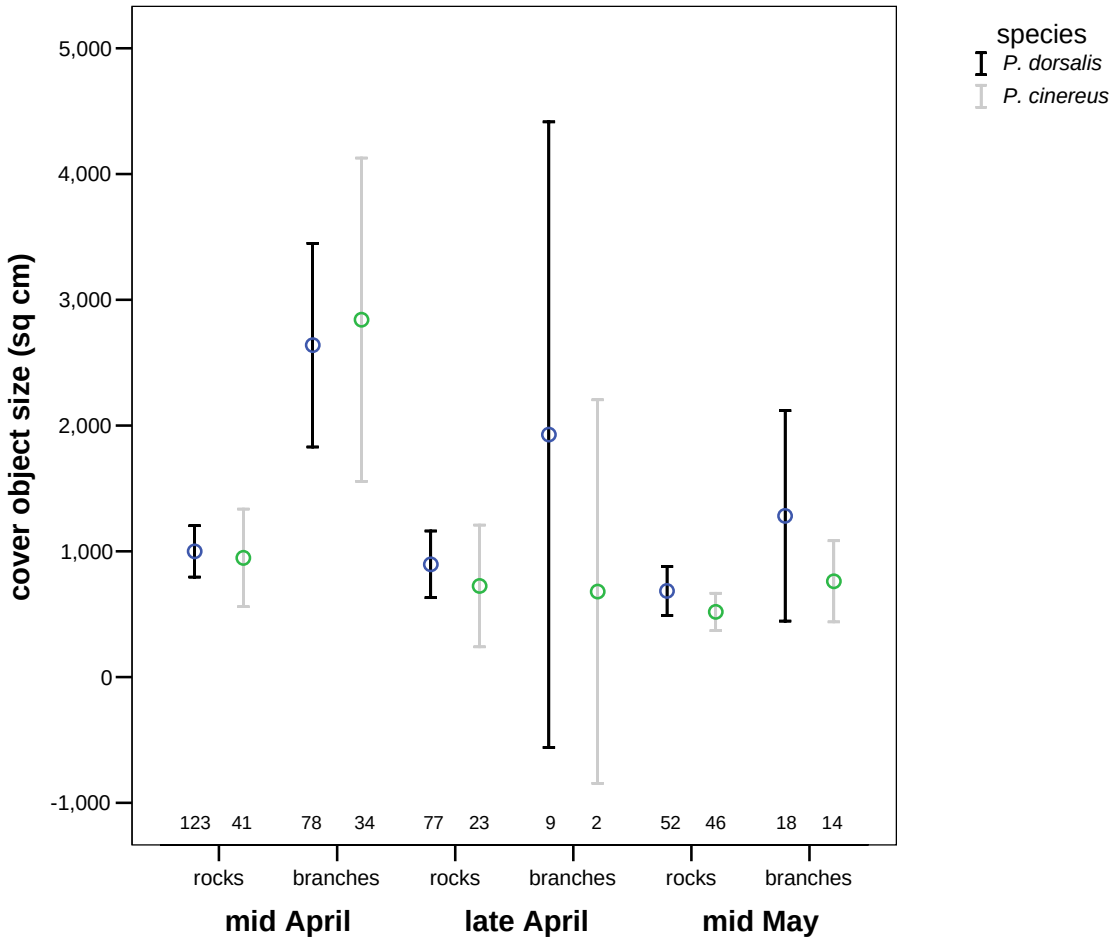

Figure 2. Size of cover objects where salamanders were captured. Error bars are 95% confidence interval. Numbers are sample sizes.

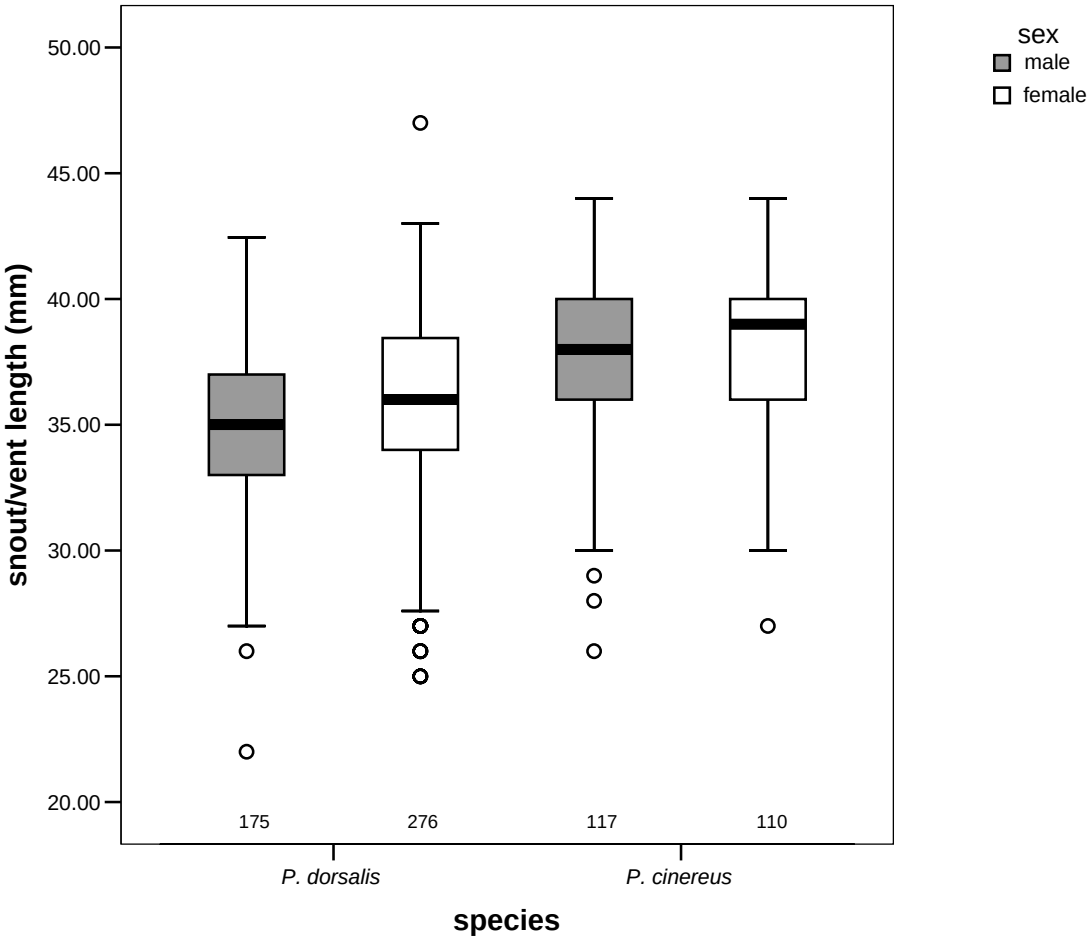

Figure 3. Comparison of adult SVL between species and sexes. Plot shows the median, interquartile range, and range. Circles represent outliers (as identified by SPSS box plot function). Numbers are sample sizes.

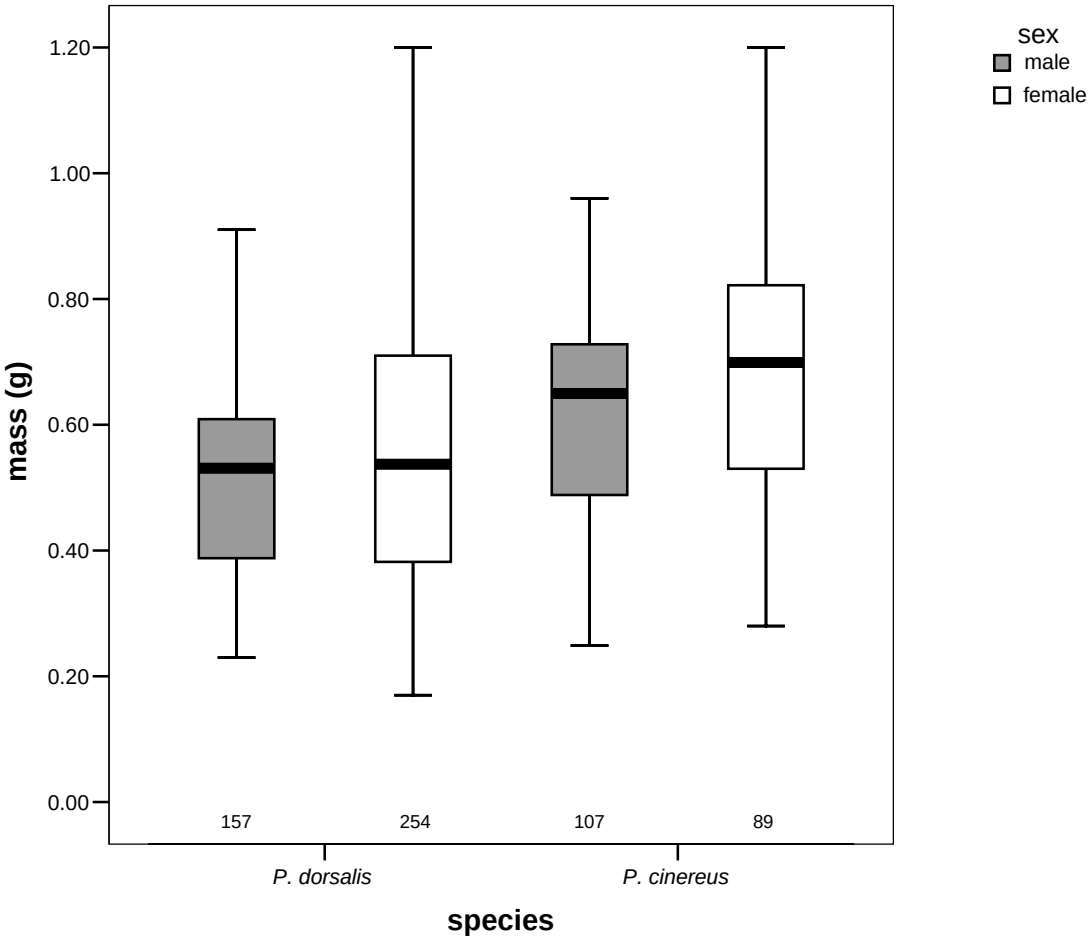

Figure 4. Differences in adult mass between species and sexes. Plot shows the median, interquartile range, and range (SPSS box plot function). Numbers are sample sizes.

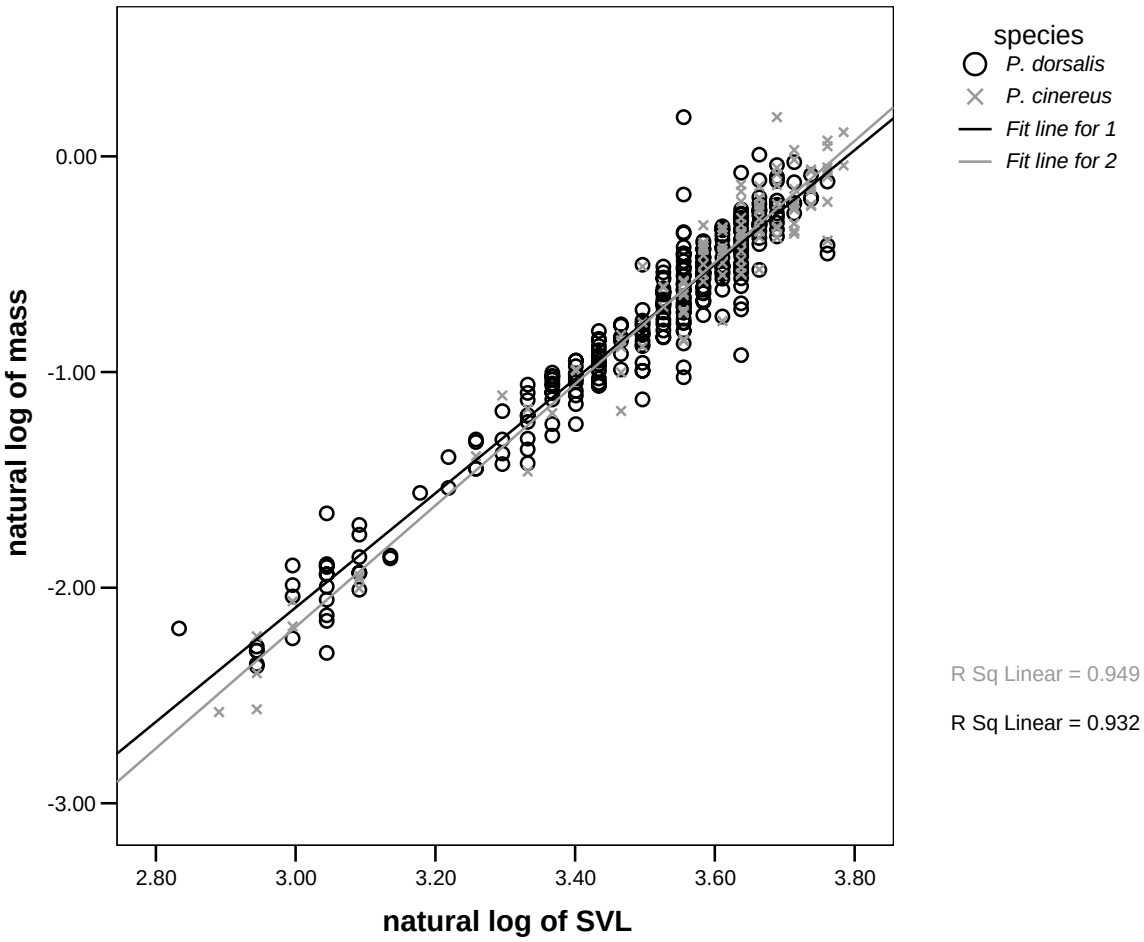

Figure 5. Relationship between mass and SVL for adults and juveniles of each species.

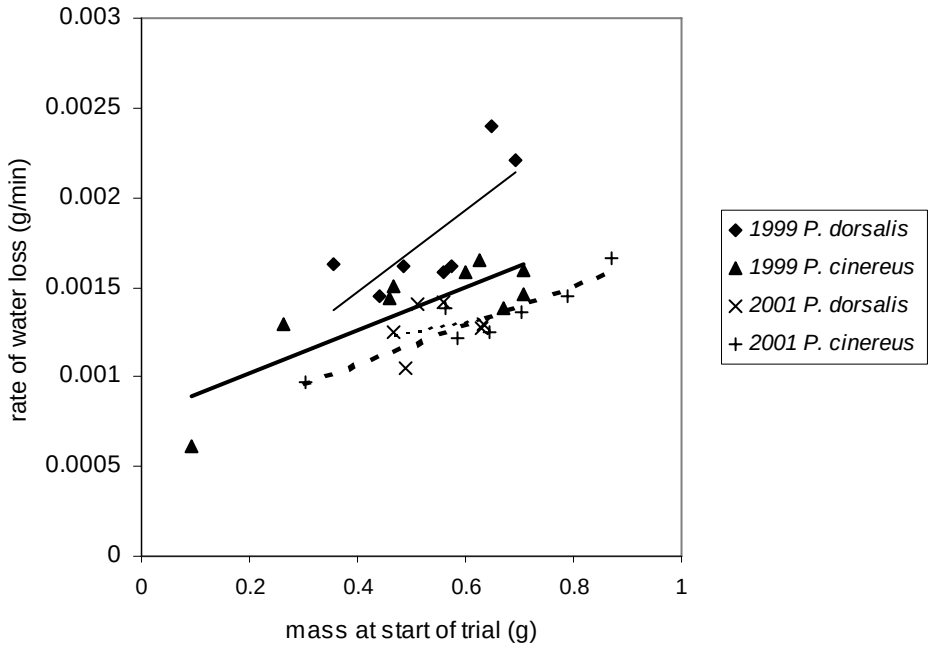

Figure 6. Rates of desiccation for each species separated by year. Solid lines are 1999 data. Dotted lines are 2001 data. Thinner lines are *P. dorsalis* data. Thicker lines are *P. cinereus* data.

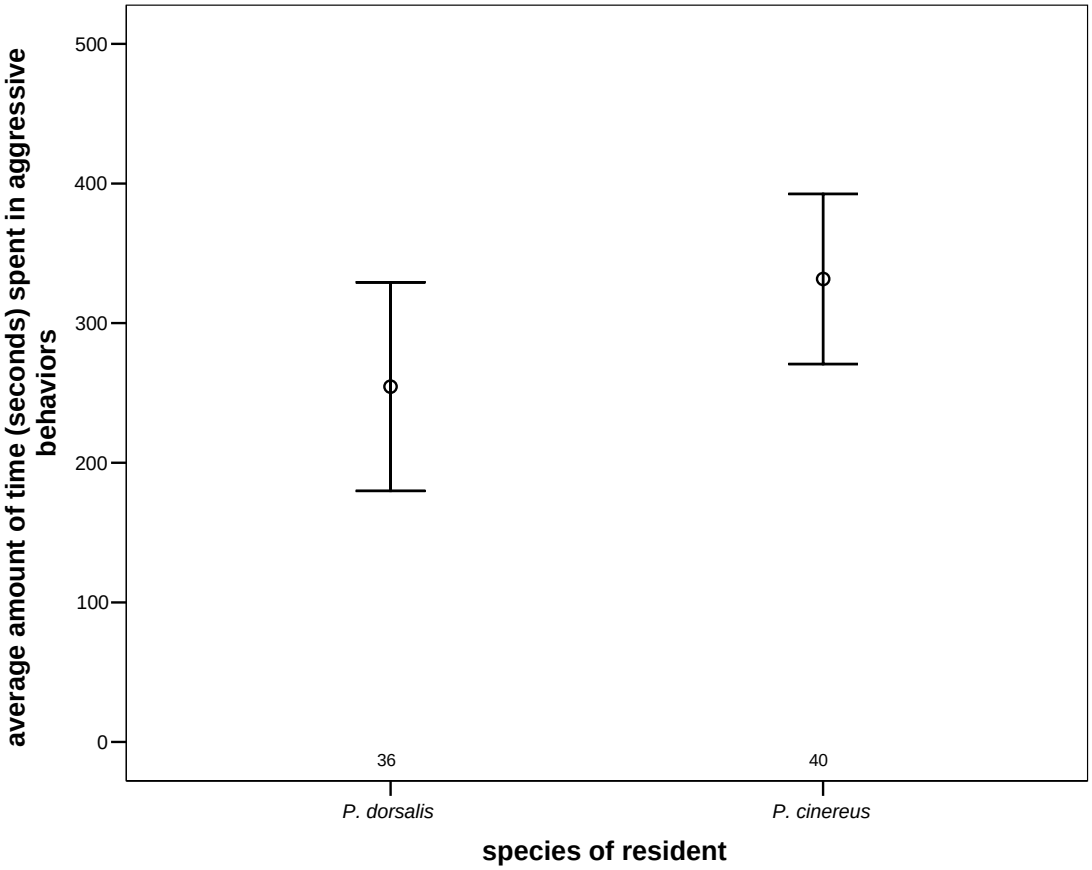

Figure 7. Mean amount of time residents spent in aggressive behaviors regardless of species of intruder. Error bars are 95% confidence intervals. Numbers are sample sizes.

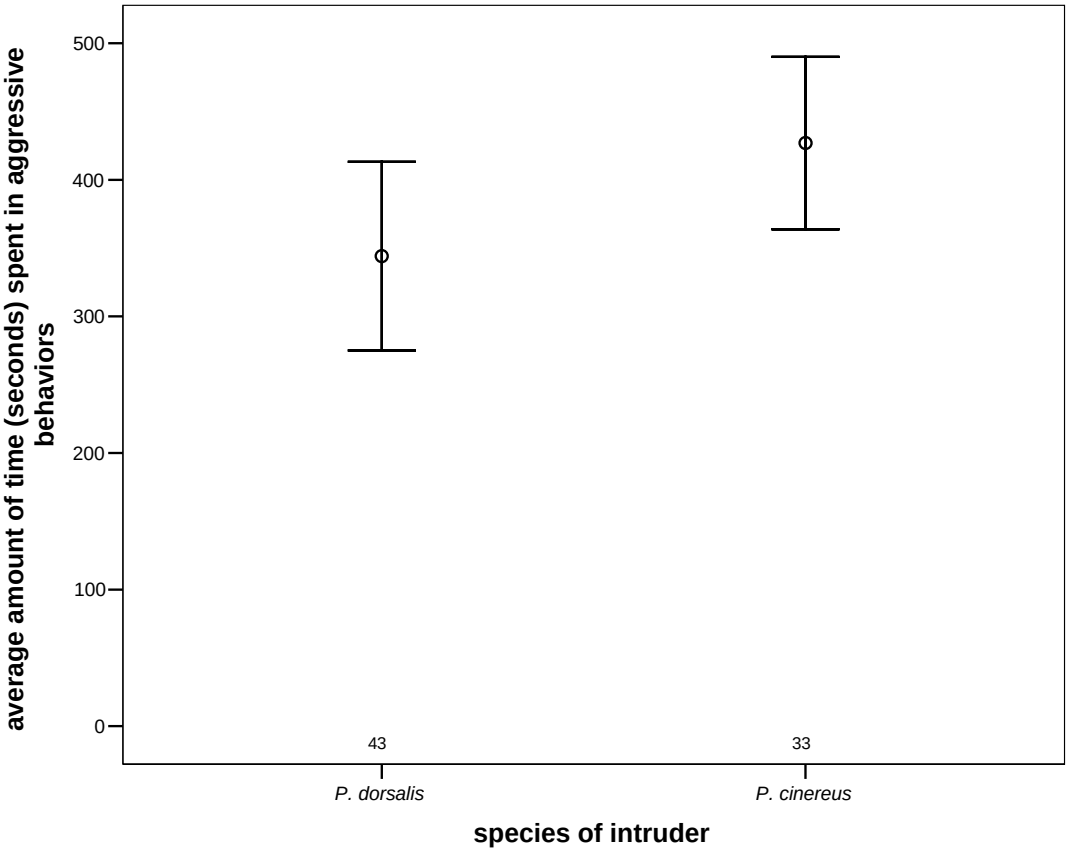

Figure 8. Mean amount of time intruders spent in aggressive behavior regardless of species of resident. Error bars are 95% confidence intervals. Numbers are sample sizes.

Nathan Murphy

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Employment

Environmental and natural resource policy analyst
Michigan Senate Democrats

Education

Indiana University, Bloomington, IN
Department of Biology
PhD in Ecology and Evolutionary Biology
School of Public and Environmental Affairs
M.S.E.S in Applied Ecology

Michigan State University, East Lansing, MI
B.S. in Social Science

Teaching Experience

Adjunct Faculty, Indiana University, Bloomington
Wetlands Natural History and Management (lab and lecture course)
Developed course outline and materials, constructed and maintained course website, provided guidance for two Associate Instructors, lectured on course material, led fieldwork groups, wrote exams, managed logistics of field course
Aquatic Habitat Analysis (lab and lecture course)
Developed course outline and materials, hired and provided guidance for two Associate Instructors, lectured on course material, led fieldwork groups, wrote exams, managed logistics of field course
Terrestrial Habitat Analysis (lab and lecture course)
Format and responsibilities the same as the Aquatic Habitat Analysis class
Co-instructor, Indiana University, Bloomington
Humans and the Biological World (lab)
Co-developed and co-taught a lab section, developed syllabus, lab activities, and assignments, graded assignments
Entomology (lab and lecture course)
Developed half of class outline and materials, developed course web site, cowrote exams, graded assignments, developed and graded student insect collection assignment, initiated in-class discussions, created hands on experiences for students in laboratory setting

Associate Instructor, Indiana University, Bloomington
Evolution

Led discussion groups, met with students, assisted in test grading, assisted in managing Undergraduate Teaching

Introductory Biology Laboratory for Science Majors (lab)

Taught a lab section, assisted in a lab section, assisted in planning lab activities, wrote exams, graded quizzes, exams and papers

Humans and the Biological World (lab for non-science majors)

Taught a lab section, assisted in a lab section, assisted in planning lab activities, graded assignments

Terrestrial Habitat Analysis
Aquatic Habitat Analysis

Assisted in planning of field activities, utilized contacts in state agencies to arrange labs with state employees, lectured on selected topics, led field work groups, arranged and provided transportation, arranged equipment use, grading

Mentoring experience

L490 Independent Undergraduate Research

Joseph Repay	graduate school, Exercise Science
Stacey Nathanson	law school
Brent Toney	graduate school, Biology
Derek Patton	Phlebotomy Lab Supervisor, Bedford Hospital
Amanda Stumpf	medical school

Honors Thesis

Patrick Evans	graduate school, Evolutionary Genetics at University of Chicago

Publications:

Gustafson, E. J., N. L. Murphy, and T. R. Crow. 2001. Using a GIS model to assess terrestrial salamander response to alternative forest management plans. *Journal of Environmental Management* 63:281-292.

Murphy, N and M. A. Watson. 1996. Sectorial root growth in cuttings of *Coleus rehneltianus* in response to localized aerial defoliation. *Vegetatio* 127:17-23.

Invited seminar

"Terrestrial Salamander communities: what allows coexistence?"
Valparaiso University, IN

Presented papers

"Differences in distribution and physiology of two species of *Plethodon*" American Society of Ichthyologists and Herpetologists. Annual Meeting.

"Distribution and coexistence of two terrestrial salamander species: a difference in desiccation physiology" Ecological Society of America. Annual Meeting.

"Terrestrial salamander differences between a normal and wet spring." American Society of Ichthyologists and Herpetologists. Annual Meeting.

"Differential distribution of terrestrial salamanders in Southern IN forests." American Society of Ichthyologists and Herpetologists. Annual Meeting.

"Differential distribution of terrestrial salamanders in Southern IN forests." Declining Amphibian Populations Task Force Meeting, Milwaukee, WI

Research grants

IU Dept. of Biology, Chair's Office Graduate Student Research (awarded $1374)

U.S. Forest Service, Collaborative Research Grant (awarded $3000)

Indiana Academy of Science (awarded $482)

Assisted with grant writing and administration as co PI
IU Dept. of Biology Undergraduate Independent Research (awarded $250)

IU RUGS Undergraduate Research Grant (awarded $750)

Invited lectures/workshops

Faculty Colloquium on Excellence and Teaching, Indiana University

"Lake Monroe Wetlands and Pelagic Ecosystems."
FACET is an excellence in teaching award for IU faculty where part of the award is a retreat for several days where exploring new fields and new ideas about teaching are encouraged.

School of Public and Environmental Affairs, Indiana University

"An Introduction to Wetlands: Science and Policy."
Given to high school students in a summer environmental science residency program, and high school teachers in a similar program.

Service

Carriage Town Historic Neighborhood Association
: President – organized and managed volunteer workdays and neighborhood events, acted as liaison to other organizations, and performed issue advocacy

Atwood Stadium Authority
: Event planning, organized and managed volunteer workdays, acted as liaison with the neighborhood

Crim Festival of Races
: Traffic control and runner assistance during Katrina victim fundraiser

Bastille Day Run
: Traffic control and runner assistance during annual races

Southern Indiana Brownies Math and Science Day
: Developed activities and concepts presented, and managed volunteers

U.S. Forest Service
: Led interpretive nature hikes focusing on local amphibians and reptiles. Assisted in construction and maintenance of native seed nursery

Political Science Dept., Indiana University, Bloomington
: Designed and conducted a field day for high school students in a summer residency program comparing different management plans of local natural areas using a multi-disciplinary approach

US Fish and Wildlife Service, Bloomington Field Office
: Collected and identified biological samples of fish, turtles, and aquatic invertebrates, collected ornithological samples, examined samples, entered and analyzed data

National Resource Conservation Service
: Wrote newsletter, developed management plans for private woodlots, assisted in developing erosion control plans, surveyed eroded sites

References

Dr. Craig Nelson	Dr. James Hengeveld	Judge Duncan Beagle
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